

A RE-CLASSIFICATION OF THE SIMULIIDAE  
(DIPTERA) OF AFRICA AND ITS ISLANDS



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## SYNOPSIS

A new supraspecific classification is proposed for the Simuliidae of the African Continent and its associated islands, based on a wider study of world forms. Identification keys and diagnoses are given for all supraspecific taxa recognized, and two new genera and six new subgenera are erected: tribal taxa are defined on a world basis. Distribution is shown (with maps) for each genus-group taxon occurring in the whole African area, and a brief summary of the bionomy is included for each subgenus found in the Ethiopian and Malagasy Regions. Comparisons are made between the genus-group taxa occurring in the African area and those in other zoogeographical regions and possible affinities discussed. A summary is given of the proposed classification in which all known African species are placed, and an alphabetical index-catalogue of all species-group names applying to the Ethiopian and Malagasy Regions is included, which shows the status and whereabouts of all types.

## INTRODUCTION

IN the late 1940's and early 1950's onchocerciasis was found to be a much more widespread and serious human filarial disease than had previously been thought, and intensive entomological work on the known or potential Simuliid vectors of onchocerciasis was begun in several parts of Africa. An initial difficulty experienced by workers in the field was the lack of any comprehensive work by which the many *Simulium* species found in tropical Africa could be readily identified, and it was to remedy this that Freeman & de Meillon (1953) prepared their monograph on the Simuliidae of the Ethiopian Region—which has remained, and will continue to be for many years, the standard treatise on the species of this area, although (apart from brief notes on larvae) it deals only with the adult and pupal stages. Crosskey (1960) on the larvae to a large extent supplements Freeman & de Meillon for this stage.

It was not germane to the main purpose of Freeman & de Meillon (1953) for them to consider the detailed classification of Simuliidae on a world basis, nor would this have been feasible at the time, since up to then no fully comprehensive works on classification had appeared even for the much better known fauna of the Holarctic Region; since then, however, a large quantum of comprehensive taxonomic work has been published from which a widely agreed world classification of the Simuliidae is beginning to emerge, and it now seems timely to harmonize the classification of African forms (particularly those from the Ethiopian Region) with that of other zoogeographical regions. To do this, I have put forward in this paper a supra-specific classification of the African Simuliidae that is based on a world review of the family and is intended to carry the work of Freeman & de Meillon (1953) a stage further; in doing so I have thought it useful to embrace the fauna of Palaeartic Africa and the islands most nearly associated with the African Continent, as well as that of the Ethiopian and Malagasy Regions (the latter is treated as distinct from the Ethiopian Region in accordance with current trends in zoogeography).

The approach is that of orthodox taxonomy using morphological characters from the adult, pupal and larval stages (the egg is devoid of taxonomic features). Micro-morphological characters of the giant chromosomes of the larval salivary glands, which are supposed to have value in unmasking cryptic species, have been little

investigated as yet for the fauna of Africa, and from work elsewhere on such cytotoxic characters there is no evidence to suggest that they can be of value above the species level in the Simuliidae : similarly the completely phenetic approach of numerical taxonomy has not been attempted in the present work, although the time is approaching in Simuliid taxonomy when the computer might be used with advantage. At present there is still much refinement of the supraspecific classification that needs to be done by conventional means, and one of the main objects here has been to consider the various segregates (or from another viewpoint, aggregates) found in the fauna of the Ethiopian and Malagasy Regions and to equate them in rank as species-groups or named genus-groups taxa with similar categories found in other regions.

The fauna of the Ethiopian Region presents some unusual difficulties in the satisfactory delimitation of segregates within *Simulium* Latreille, the preponderant genus in the region, which I am convinced should be maintained in its old broad sense with subdivision below the generic level, because of the occurrence of many species in which one or another stage is aberrant (so that there is a lack of congruence between adult and immature forms). This phenomenon occurs especially in the curious phoretic forms which live as larvae and pupae in obligatory association with crabs or mayflies, for in these the immature stages (presumably in adaptation to the unique ecology) are often atypical in many characters, although the adults are normal, but several free-living species also are unexpectedly disjunct between the stages : as examples, *Simulium wellmanni* has the immature stages normal for the group to which it clearly belongs but has an exceptional male hypopygium with multiple style spinules quite unlike that of its congeners, and *Simulium albivirgatum* has adults and pupae essentially similar to those of its obvious allies but has a completely different and unique larval stage. Because of such incongruence between the developmental stages it is not always easy to define subgenera or species-groups in a way which is completely satisfactory for both sexes, pupae and larvae, and some segregates are more easily recognized in one stage than another ; but so far as possible the diagnoses given have been framed to cover all variants that may occur in all stages of the included species. Subgenera are defined by combinations of characters from all stages, but I have tended to attach greatest weight to differences or resemblances among adults and to consider aggregates of species as consubgeneric if no adult differences exist, for if completely equal weight is attached to characters of all stages (as Davies, 1965 : 167, considers best for erection of black-fly genera) it results in too much taxonomic value being attached to the occasional aberrant larval feature (such as the short flat mouth-brush of *Simulium copleyi* or unique hypostomium of *S. bernerii*), to bizarre forms of pupal gill or to an aberrant pupal abdominal onchotaxy (such as that of *S. lumbwanum*). Within subgenera, however, there are species-groups that are best distinguished on features of the immature stages, often the pupal gill.

Although this paper is concerned primarily with classification above the species level, and not with the identity of species among themselves, it is necessary to allude briefly to my treatment of the pupal forms as recognized by Freeman & de Meillon

(1953) because they are enumerated in the 'Included taxa' section under each genus, subgenus or species-group of *Simulium* as appropriate, and are listed in the summary of the proposed classification. Freeman & de Meillon (op. cit.) when working out the Ethiopian fauna were faced with the fact that almost identical or at least very similar adults are often associated with pupae in which the form of the gills differs conspicuously and rather constantly, and in order to express this in taxonomy introduced the concept of the 'pupal form' (though there had been some previous use of the term 'variety' for forms with slight gill differences): all forms were treated as conspecific if the adults were not distinguishable, and the single species regarded as polymorphic in the pupal stage. Workers in other regions had usually treated wide differences in pupal gill as evidence that different species were involved, even if the larvae and adults were not readily distinguishable, as for instance with *Simulium (Wilhelmia) equinum* (L.) and *S.(W.) salopiense* Edwards. There is still no means of 'proving' whether forms in the sense of Freeman & de Meillon (1953) are pupal polymorphs within a species, or whether the differing pupae are those of biologically distinct species, but since there are small consistent differences also in associated larvae, and I suspect in adults if studied sufficiently, I think it preferable to regard all the pupal forms tentatively as distinct species (at least until clear evidence is forthcoming to show otherwise): I therefore cite the names of all of them in specific status wherever they occur in the paper, but have used the term 'Included Taxa' (in preference to the more usual 'included species') to emphasize the element of doubt about the status of some of the inclusions.

The following points should be noted about the geographical and bionomic information given:

The distribution maps for the subgenera are based on known localities (shown by circle or triangle symbols) for all included species derived from material seen and published records; the approximate limits of subgeneric distribution are shown by a solid line. The maps show certain areas within the presumed range but for which information is lacking: the main ones are indicated by question marks. For Palaearctic subgenera that occur in Africa the distribution is only shown on the maps for the Mediterranean area.

Although some species are very catholic in their choice of breeding site or in female host preference there is a clear tendency for the constituent species of any subgenus to have similar ecological requirements for the early stages and a similar female host choice, and therefore for one subgenus to differ characteristically in behaviour from another. A brief summary of the main features of the bionomy has been given for each subgenus found in the Ethiopian and Malagasy Regions, but it must be appreciated that these are generalizations for the subgeneric taxon as a whole to which exceptions may occur in individual species.

The text-figures given illustrate the main characters found in the supraspecific taxa recognized, and show the range of form occurring within a taxon when there is considerable variability (as in the pupal gill). Some figures, especially of the pupal gill, have for convenience been redrawn from Freeman & de Meillon (1953) or from the same slides as were used by these authors.

The genus-group name *Hagenomyia* Shewell used in the discussion of *Tetisimulium* Rubzov (p. 106) is a preoccupied homonym for which a replacement name will be given in a later paper.

#### MATERIAL STUDIED

This paper is based primarily on a study of the Simuliidae in the collection of the British Museum (Natural History), which is especially comprehensive for the fauna of Africa. My own collections from Nigeria and Uganda, together with a large amount of material sent to me by workers in Africa and associated islands during the past ten years, has also been studied and will now be incorporated into the British Museum collection. Material on loan has been seen from the South African Institute for Medical Research, Johannesburg. Extra-limital material of New World and Palaearctic forms, required for comparative purposes, has been received during preparation of the paper from the United States National Museum, Washington and from the Zoological Institute, Academy of Sciences, Leningrad, through the courtesy of specialists named in the Acknowledgments, and is now in the BMNH collection.

#### TAXONOMIC CHARACTERS AND THEIR TERMS

Morphological features of value for supraspecific classification exist in the adult, pupal and larval stages : there are no taxonomic characters on the egg.

*Adult characters.* Characters of the adult wing, legs, thorax and male hypopygium with their terms are shown in Text-figs. 1-6, and the structures of the female terminalia in Text-figs. 162 & 163. It will be noted that in order to give continuity of usage with the monograph of Freeman & de Meillon (1953) the same terms have been used for parts of the male hypopygium and female terminalia, although some of this terminology is suspect to the morphological purist : it appears useful to continue the usage of coxite and style for its simplicity in taxonomy. The main basally bicornuted plate of the female sucking-apparatus is here termed the *cibarium* in accordance with the usage of Wenk (1962) ; the area between the cornuae, termed the pharyngeal bar by Freeman & de Meillon, may be simple and straight or smoothly rounded (here characterized as 'unarmed') or it may bear blunt or prominent denticles. The groove separating the lower part of the mesothorax (katepisternum) from the upper parts in both sexes has been found to be of major taxonomic value and has been termed the *mesepisternal sulcus*. New taxonomic characters discovered in the present work on the posterior surface of the adult head have necessitated the use of the terms shown in Text-figs. 57-60 : the term *postgenal lobe* is adopted from the morphological work of Wenk (1962), and the term *postgenal membrane* is introduced for easy reference to the non-sclerotized area in the mid-line lying between the postgenal lobes.

*Pupal characters.* The paired branched or variously modified prothoracic organs are physiologically gills, and the simple term *gill* is here used in preference to the term respiratory organ used by Freeman & de Meillon (1953). Gill form provides a useful character aggregating forms into species-groups, but the gills of forms that are

clearly close relatives may assume widely differing and sometimes bizarre shapes, and the gill form cannot normally be used as a major differential character between genus-group segregates. The form of the terminal abdominal hooks or tubercles and the form and degree of sclerotization of the abdominal cuticle provide some useful characters ; and the presence or absence of transverse rows of backwardly-directed irregular spiny processes situated anterodorsally on the dorsum of the last few abdominal segments is often of major taxonomic importance (for brevity and simplicity these have been termed *spine-combs* throughout the text : see Text-fig. 168). In addition to the spine-combs (if present) the pupal abdomen has a rather constant arrangement of main hooks on the dorsum and venter for which the term *onchotaxy* is here used : in general the onchotaxy has a fixed basic plan in each genus which may or may not be supplemented by supernumerary small fine hooklets or variously modified setae, the form and arrangement of which may be of taxonomic value. Some island and phoretic forms show extraordinary aberrant departures from the normal basic onchotaxy.

*Cocoon characters.* The discreteness of form, modifications of shape and closeness of weave (for instance, presence or absence of fenestration) of the cocoon provide important taxonomic characters which can be of use at species-group or superior level. In some primitive forms the cocoon material forms almost a communal matrix, but most often each pupa is invested individually in its own discrete cocoon with definite shape : this is termed *slipper-shaped* if the cocoon is simple and lacks a neck or collar connecting the two slides anteriorly (Text-figs. 164 & 166) and *shoe-shaped* if the two sides of the cocoon are connected anteriorly by a raised neck or collar (Text-figs. 165 & 167). Reduction of the cocoon to cover only the pupal abdomen or to a mere few threads and a holdfast may occur, and provide a taxonomic feature for rare groups ; likewise, incorporation of inorganic matter in the texture of the cocoon is associated with some taxa and not others. The presence of a simple or divided anterodorsal median projection from the body of the cocoon is sometimes a species-group character.

*Larval characters.* The morphology of the Simuliid larva and a detailed discussion of the characters of taxonomic value was given in my earlier paper on the larvae of Ethiopian black-flies (Crosskey, 1960). The terms used for larval characters are the same as in the previous work and are shown on the accompanying Text-figs. 7-15. The head pattern is described as *negative* when the spots themselves are pale with dark infuscation around them (Text-figs. 232-234), and as *positive* when the spots are dark (Text-figs. 235-240). The larval body shape and the cuticular ornamentation of variously modified setae (when present) provide useful characters at species-group or genus-group level. In the hypostomium the rows of hypostomial setae may either lie subparallel to the sides of the hypostomium (as Text-fig. 303) or they may diverge from the hypostomial margins posteriorly (as Text-fig. 304) and this character tends to divide certain groups of genus-group taxa from others. Particular attention should be drawn to the *comb-teeth* of the mandible (Text-fig. 13) : these are three in number and lie immediately basad of the main apical tooth ; their size relative to each other and their degree of differentiation from the apical teeth or from

the spinous comb that precedes them provide useful characters, since they differ between taxa. In the mature larva of some forms the cervical sclerites are linked by continuous (although sometimes weaker) sclerotization to the upper ends of the postocciput (Text-fig. 20), but in the majority of forms they form small discretely isolated platelets in the neck membrane (Text-figs. 14 & 21).

The shape of several morphological structures of the larva (such as the head sclerites, hypostomium and postgenal cleft) alters during larval development, and the number of several other structures increases (such as the number of cephalic fan rays, antennal segments, cuticular setae, and hooks in the posterior circlet) : it must be emphasized, therefore, that the larval characters cited in the keys and diagnoses throughout the text are those of mature or almost fully developed larvae.

#### GEOGRAPHICAL DISTRIBUTION OF SIMULIIDAE IN AFRICA AND ITS ISLANDS

The family Simuliidae is found throughout continental Africa wherever suitable watercourses exist for the pre-imaginal stages. It is only absent completely from areas of utter desert (most of the Sahara and Kalahari deserts). The family is known from all but three of the African states : there are no records as yet from the arid desert states of Libya, Spanish Sahara, and Mauritania. In the Arabian peninsula Simuliidae occur in South Yemen Republic (near the Yemen border), but are unknown from the Hadhramaut.

In the islands around Africa the distribution of Simuliidae is as follows : present in the Canary Islands, Fernando Po, St. Helena, Madagascar, Comoro Islands, La Réunion, Mauritius, Rodriguez and the Seychelles ; absent from Ascension Island, Tristan da Cunha, Gough Island and Aldabra ; unknown from the Cape Verde Islands, Principe, São Thomé, Annobon and Socotra (but none of these islands surveyed for Simuliidae).

Simuliidae in North (Palaeartic) Africa reach a southern limit at about 30°N. (in Morocco), and in Ethiopian Africa reach a northern limit at about 15°N., except down the valley of the Nile where the Ethiopian fauna penetrates northwards to about 25°N. ; but between these latitudes, which approximately delimit the desert, Simuliidae are recorded from two central Saharan massifs (Tibesti and Tassili des Ajjer).

The altitudinal range of Simuliid breeding in Africa is from sea-level to 14,700 ft. and altitude in general is not a significant factor in determining distribution, which appears to be governed primarily by geological considerations—for the geological history has determined the geographical position and hydrological characteristics of the river and stream systems that are suitable for development of the immature stages. Thus, in the detailed picture of distribution, Simuliidae are found to be present most evidently in areas where the Precambrian basement rocks of Ethiopian Africa form the land surface and give rise to rocky-bedded rivers and streams ; in other areas where marine incursions have overlaid the Precambrian basement with sedimentary deposits of much later periods (usually Cretaceous and Tertiary) the watercourses tend to be sandy or muddy and Simuliidae absent or less universally

present. In the case of the islands black-flies are absent from those which are devoid or almost devoid of running water (Ascension, Tristan da Cunha, Aldabra) but are abundant—though very limited in number of species—in those which are well-watered by numerous cascading streams (St. Helena, Seychelles, La Réunion). (How the Simuliidae have reached such remote islands can only be conjectured but it is notable that the forms that have done so almost all possess a large tooth basally on the claws of the female, characteristic of ornithophilic species : carriage on birds is the most plausible explanation, though we lack evidence that black-flies can survive for more than a very brief period on avian hosts.)

CHARACTERISTICS AND AFFINITIES OF THE SIMULIID FAUNA OF THE  
ETHIOPIAN AND MALAGASY REGIONS

The Simuliid fauna of North Africa and the Canary Islands is entirely typical for the Palaearctic Region, and is therefore only very briefly considered further below, but a more detailed review of the main zoogeographical features and possible affinities of the Simuliidae of the Ethiopian and Malagasy Regions is given in order to show how the fauna of these regions fits in the world picture (and to assist workers in other areas to whom a digest of the principal characteristics of the African fauna might be useful for comparative purposes).

All genus-group taxa and many of the species in North Africa are shared in common with the Simuliid fauna of western Europe, and most with the Canary Island fauna also : the best represented segregates are *Eusimulium*, *Wilhelmia* and *Odagmia*. Only one species found in North Africa occurs also in the Ethiopian Region : this is *Simulium* (*Eusimulium*) *ruficorne* with the widest distribution of any African black-fly, occurring through North Africa (Morocco to Tunisia), in Egypt and Middle East, the whole Ethiopian Region (including southern Arabia), and the Malagasy Region including the Mascarene islands ; the Palaearctic and Ethiopian distributions of *ruficorne* are interlinked by the occurrence of this species in the mid-Sahara massifs of Tibesti and Tassili des Ajjer, and it is impossible to be certain whether *ruficorne* is to be seen as a Palaearctic species that has spread throughout the other regions or as an Ethiopian element that has penetrated into the southern Palaearctic Region.

The Malagasy Region (including the Seychelles and Mascarene islands) has a very limited Simuliid fauna in which the more primitive Prosimuliini are, so far as is known, completely absent and in which three subgenera of *Simulium* s.l. are the only genus-group taxa represented : of these *Eusimulium* is almost cosmopolitan, *Pomeroyellum* is an Ethiopian segregate that has clearly reached Madagascar from the African mainland, and the third (*Xenosimulium* sgen. n.) is endemic, but has many characters in common with two of the subgeneric segregates in the Ethiopian Region and may have derived also from forms that originated from Africa. One species in Madagascar (*starmuhlneri*) has characters resembling some forms of *Morops* from New Guinea, but convergence is presumed, and there is no evidence of close affinity between the Malagasian fauna and that of the Oriento-Australasian Regions : the endemic subgenus *Xenosimulium* sgen. n. shows many resemblances

to *Grenierella* in South America, but again convergence seems likely, and balance of evidence points to an African origin for the Malagasy fauna.

The most striking feature of the rich Simuliid fauna of the Ethiopian Region is its endemism: apart from *ruficorne* mentioned above, which occurs also in the Palaearctic and Malagasy Regions, and with the possible exception of *buckleyi* which has been identified from Madagascar, there are no Ethiopian species that occur outside the region, and almost all the subgeneric taxa are endemic (though often with apparently related or parallel segregates in other regions). As with all other regions except the Oriental Region (from which the Prosimuliini are absent on present evidence) the fauna is an admixture of relatively primitive Prosimuliine forms and of supposedly more advanced Simuliine forms, but in the Ethiopian Region the Prosimuliine fauna is very impoverished and in number of species accounts for only about 8% of the fauna (much less than in the Holarctic Regions, and less than in South America—where, assuming that *Gigantodax* is included, about 14% of species-composition of the fauna is Prosimuliine): the overwhelming majority of Ethiopian forms, as elsewhere in the world tropics, belong to *Simulium* s.l.

The Prosimuliine forms in the Ethiopian Region (in the present work all placed in the genus *Prosimulium* s.l. but in the past assigned to *Cnephia*) appear to be relict remnants of a *Prosimulium*-like fauna that was once widespread throughout Africa, or such is the impression given by the few and widely scattered loci from which these few presumed primitive forms are yet known. The morphological characters of *Prosimulium* in the southern tip of the Ethiopian Region are slightly more 'advanced' than those of *Prosimulium* in Palaearctic Africa (in the sense that spiniform costal macrotrichia are developed and the fork of *Rs* obliterated) but geographically intermediate forms (known from Uganda and Rhodesia) are also morphologically intermediate, and there is no real faunal break between Palaearctic and Ethiopian *Prosimulium*; there is no evidence to suggest that Ethiopian Prosimuliine forms had a southern route of entry into Africa.

Throughout most of the Ethiopian Region the only genus present in the black-fly fauna is *Simulium* in the wide sense, and over 90% of Ethiopian species belong in the genus. In the present re-classification ten subgenera are recognized in the Ethiopian *Simulium* fauna, of which eight are endemic and confined to the region (*Pomeroyellum*, *Meilloniellum*, *Lewisellum* sgen. n., *Phoretomyia* sgen. n., *Anasolen*, *Freemanellum* sgen. n., *Metomphalus* and *Edwardsellum*), of which one occurs in the Holarctic Regions as well as the Ethiopian (*Byssodon*), and of which one is cosmopolitan or almost so (*Eusimulium*). It is of interest to note that the number of subgenera in the Ethiopian Region here accepted as valid (10) conforms closely to the numbers in the Nearctic and Palaearctic *Simulium* fauna: Stone (1965), for the smaller fauna of North America, accepts nine subgenera, and Rubzov (1959–1964)—though ranking them as full genera—recognizes eleven genus-group segregates in *Simulium* sensu lato in the Palaearctic Region: thus there is close taxonomic balance in the categories which it is considered desirable to recognize as named segregates of *Simulium* s.l. between the present reclassification for the Ethiopian Region and the classifications already existing for the Holarctic area. The *Simulium*

fauna in the Oriental and Australasian Regions is much smaller than that in each of the other regions, and four subgenera have been recognized for the Australasian (Crosskey, 1967a) : there is no recent revisionary work on the Oriental fauna but from a preliminary study on this region it appears that almost all described forms are assignable to only three subgenera (*Eusimulium*, *Gomphostilbia* and *Simulium* s. str.). No complete subgeneric classification has yet been worked out for the very large *Simulium* fauna in South America (approximately 200 species : Vulcano, 1967).

A conspicuous feature of the world *Simulium* fauna is that different regions sometimes show segregates of forms that conform with each other in a large number of characters but differ clearly in some others, the morphological similarity often being accompanied by ecological preferences for a similar aquatic environment for the immature stages. There is insufficient evidence to show whether the resemblances are due to recent monophyletic relationship or whether convergence exists, perhaps partly at least from adaptation to particular ecological niches, and it is best to regard such pairs of closely similar yet slightly differing segregates as 'counterparts' in the different zoogeographical regions—since no clear conclusion can be drawn as to how the similarity arose. In the Ethiopian Region several of the endemic subgenera recognized have 'counterpart' subgenera of the nature just described in other regions, and to help towards a world picture of such resemblances the following list summarizes the counterparts :

Endemic Ethiopian subgenus	Counterpart subgenus
<i>Pomeroyellum</i> Rubzov	<i>Morops</i> Enderlein (Australasian Region)
	<i>Psilopelmia</i> Enderlein (Neotropical Region)
<i>Anasolen</i> Enderlein	<i>Grenierella</i> Vargas & Diaz Najera (Neotropical Region)
	<i>Xenosimulium</i> sgen. n. (Malagasy Region)
<i>Freemanellum</i> sgen. n.	<i>Grenierella</i> Vargas & Diaz Najera (Neotropical Region)
<i>Metomphalus</i> Enderlein	<i>Wilhelmia</i> Enderlein (Palaeartic Region)
<i>Edwardsellum</i> Enderlein	<i>Wilhelmia</i> Enderlein (Palaeartic Region)

The resemblances and differences between these counterparts are detailed later in the text under the treatment for each Ethiopian subgenus mentioned. There are no counterpart subgenera in other regions to the Ethiopian subgenera that live in phoretic association with crabs (*Lewisellum* sgen. n.) or nymphal mayflies (*Phoretomyia* sgen. n.) or to the subgenus *Meilloniellum* Rubzov, to which both the phoretic subgenera are apparently closely related : the phenomenon of phoresy with river-crabs occurs only in tropical Africa, and phoretic associations with mayflies (although recorded from the Oriental Region and Soviet Asia) are almost unique to the Ethiopian Region, making the Ethiopian *Simulium* fauna especially remarkable for the evolution of such exceptional behaviour.

If it is assumed, as seems probable from their suites of characters, that *Pomeroyellum*, *Meilloniellum*, *Lewisellum* and *Phoretomyia* are in general closely related to *Eusimulium*, and that *Metomphalus* and *Edwardsellum* have close affinity with *Wilhelmia*, it then follows that the overall affinities of the Ethiopian fauna of

*Simulium* s.l. lie mostly with the Holarctic Regions ; certainly none of these subgenera suggests any close relationship with the Neotropical fauna, with the exception of some possible affinity between *Pomeroyellum* and *Psilopelmia*. The remaining trio of subgenera, *Anasolen*, *Freemanellum* and the Malagasy *Xenosimulium* are much more problematical since they have few if any features that strongly suggest affinity with the Holarctic fauna ; on the other hand they have conspicuous resemblances to some South American forms, and there *may*—though this must be entirely conjectural—with this group of subgenera be a zoogeographical connection between Ethiopian Africa and the Neotropical Region.

Finally, it may be helpful in this section to draw attention to some characters which are either always present, or alternatively which never occur, in the Simuliidae of the Ethiopian Region :—

- ♂ head always holoptic (none dichoptic, as are a few Neotropical forms).
- Antenna always II-segmented.
- Head always without postocular bulla.
- Wing-vein  $Cu_2$  never straight (cf. South American *Gigantodax* Enderlein).
- Cocoon present, always covering at least the pupal abdomen.
- Larvae always with cephalic fans.
- Larval anal sclerite always present, X-shaped.

### SIMULIIDAE Newman

SIMULIITES Newman, 1834, *Ent. Mag.* 2 : 387. Type-genus : *Simulium* Latreille, 1802.

A definition of the Simuliidae among the families of Diptera, and a more detailed consideration with diagnoses of the subfamilies, will be given in a forthcoming paper on the classification of world forms, but it may be briefly mentioned here that—in agreement with Smart (1945)—it is considered that only two subfamilies should be recognized. The first is the Parasimuliinae, containing only the single remarkable genus *Parasimulium* Malloch from western United States, and the other—the Simuliinae—comprising all other known black-flies. The subfamily Gymnopauidinae, which Rubzov (1956, 1959–1964) proposed and treated as distinct from the Simuliinae for the Holarctic genera *Gymnopais* Stone and *Twinnia* Stone & Jamnback, does not seem to me to be sufficiently distinct from other simuliids to justify subfamily rank, despite the remarkable larvae (in which all instars lack cephalic fans and the abdomen has a Y-shaped in place of the normal X-shaped anal sclerite) ; in fact, as Shewell (1958) points out, *Twinnia* is so close to *Prosimulium* Roubaud in many of its characters that there is doubt as to whether separate generic status is justified. Certainly *Twinnia* interconnects *Gymnopais* and *Prosimulium*, and makes it impossible justifiably to separate the first two off as a distinct subfamily : hence *Gymnopais* and *Twinnia* are here regarded as forming part of the tribe Prosimuliini (the more primitive one of the two tribes into which the subfamily Simuliinae is here divided). Neither *Gymnopais* nor *Twinnia* occurs in Africa and these genera are not considered further at this time.

Two tribes are here recognized in the Simuliinae, the Prosimuliini containing the

supposedly more primitive forms and the Simuliini containing the supposedly more specialized forms (in which, among other features, there has been a reduction of hairing on the radius, the development of a pedisulcus, increasing complexity with development of teeth on the male ventral plate, development of a discrete cocoon). No hard and fast line can be drawn between the two tribes, and no single character exists that will hold for distinguishing every form in one tribe from every form in the other; nevertheless, on total suites of characters there is a definite and apparently natural cleavage between two major aggregations of forms, and Prosimuliini and Simuliini are the nomenclaturally correct names to apply to the two taxa ranked at tribal level. Full diagnoses for the two tribes are given later in this paper.

In the area of Africa and its islands falling within the purview of the present revision four genera of Simuliidae occur, of which one is placed in the Prosimuliini and three in Simuliini. The Prosimuliine genus *Crozetia* Davies from the Crozet Islands in the South Indian Ocean is excluded from consideration as it is an element of the sub-Antarctic fauna having no affinity at all with any forms in the Malagasy Region. A key to the four genera is given below.

#### KEYS TO THE GENERA OF SIMULIIDAE IN AFRICA AND ITS ISLANDS

##### ADULTS

- 1 Pedisulcus absent. Basal cell present, usually quite distinct (Text-fig. 1). Costa sometimes without spiniform macrotrichia. Basal section of radius always haired. Katepisternum in profile about as deep as its length, delimited by rather broad mesepisternal sulcus, the sulcus often evanescent anteriorly (Text-figs. 16, 18) . 2
- Pedisulcus present. Basal cell absent. Costa with spiniform macrotrichia as well as hairs. Katepisternum in profile longer than its depth (Text-fig. 19), delimited by a deep narrow and more or less complete mesepisternal sulcus (Text-fig. 17) . 3
- 2 Pleural membrane haired. Style of ♂ hypopygium with one apical spinule. Calcipala undeveloped. Costa with spiniform macrotrichia and vein *Rs* simple. [North Africa] . . . . . **METACNEPHIA** gen. n. (p. 26)
- Pleural membrane bare (but in *morotoense* a few hairs present on upper mesopleuron just below scutal ridge.) Style of ♂ hypopygium with multiple apical spinules (numbering 3-9, Text-figs. 31-33). Calcipala often moderately developed (Text-figs. 23-25). Costa sometimes without spiniform macrotrichia and sometimes with *Rs* forked. [North Africa and Ethiopian Africa] . . . . . **PROSIMULIUM** Roubaud (p. 17)
- 3 Calcipala present, very well developed. Wing membrane with normal microtrichia (Plate 1A), easily visible at  $\times 100$ . Last segment of maxillary palp long and slender, much longer than preceding segments (Text-figs. 69). Posterior surface of head normal (Text-figs. 57, 59), postgenal membrane narrow and postgenal lobes angulate at ventral edge of foramen, continuous sclerotization between cardines. Basal section of radius haired or bare. [Widespread throughout area].  
**SIMULIUM** Latreille (p. 34)
- Calcipala almost absent (Text-fig. 306). Wing membrane with extraordinarily reduced microtrichia (Plate 1B), wing surfaces appearing totally bare at magnifications of  $\times 100$  or  $\times 150$ . Last segment of maxillary palp not longer than either of the two preceding segments (Text-fig. 305). Posterior surface of head abnormal (Text-figs. 58, 60), postgenal membrane broad and postgenal lobes not sharply angulate near lower corners of occipital foramen, head widely membranous between the cardines. Basal section of radius bare. [Southern Africa only]  
**AFROSIMULIUM** gen. n. (p. 30)

## PUPAE

- 1 Last abdominal segment with a pair of very long strong terminal hooks (Text-figs. 42-44). Abdominal cuticle with distinctly sclerotized tergal and sternal plates, conspicuous by pale yellowish brown colour in cast pupal pelt. Sides of abdomen often with discretely formed pleurites. Mid venter of segments 6 and 7 (sometimes also 8) with semi-membranous longitudinally striate areas dividing the sternal plates. . . . . **PROSIMULIUM** Roubaud (p. 17)
- Last abdominal segment without long terminal hooks but with a pair of very small blunt or at most slightly thorn-like tubercles. Abdominal cuticle forming mainly a delicate transparent pellicle without strong sclerotization, cast pupal pelt showing brownish plates only on the last segment or weakly on the dorsum of the first few segments. Abdomen without pleurites. Mid venter of segments 6-8 without conspicuous longitudinally striate area . . . . . 2
- 2 Sides of last two abdominal segments with complex biramous anchor-like spinous hooklets, sometimes variously multifid (Text-fig. 35). Gill arborescent. [North Africa]. . . . . **METACNEPHIA** gen. n. (p. 26)
- Abdomen completely without anchor-like hooklets. Gill of varied form . . . . . 3
- 3 Gill with three elongate tapering and flattened branches (Text-figs. 223). Abdominal dorsum without spine-combs. [Southern Africa only] **AFROSIMULIUM** gen. n. (p. 30)
- Gill not of this form (except in some *Byssodon*). Abdominal dorsum with or without spine-combs on segments 6-9. [Widespread throughout area] **SIMULIUM** Latreille (p. 34)

## LARVAE

[Note: the larva of *Afrosimulium* is unknown and the generic key cannot therefore be complete for the larval stage]

- 1 Postgenal bridge incomplete, divided by long anteriorly tapering postgenal cleft that broadly reaches the hypostomium (Text-fig. 36). [North Africa] **METACNEPHIA** gen. n. (p. 26)
- Postgenal cleft not broadly reaching the hypostomium, postgenal bridge therefore complete medially even if reduced to narrow strip . . . . . 2
- 2 Hypostomium with large, often rather fusiform, teeth aggregated into three main groups (Text-figs. 46, 49-52), sometimes only median tooth very prominent (Text-fig. 53). Cervical sclerites merged with upper ends of postocciput in band of continuous sclerotization (Text-fig. 20). Mandible with third comb-tooth enormously enlarged (Text-figs. 54, 55) and inner edge usually with long saw-like series of mandibular serrations. Maxilla with conspicuous dark dense hair tuft near base of palp (Text-fig. 56). Cephalic apotome with positive head-spots and widest some way before hind margin (Text-fig. 48). Third antennal segment much darker pigmented than remainder of antennae (Text-fig. 47). Abdominal cuticle bare. Rectal gills simple . . . . . **PROSIMULIUM** Roubaud (p. 17)
- Hypostomium not of this form, teeth not exceptionally produced and usually not so aggregated. Cervical sclerites discrete and isolated from postocciput (Text-fig. 21). Mandible with third comb-tooth not enlarged like this and inner edge without saw-like series of serrations (almost always two serrations, rarely reduced to one or obliterated, very rarely one or two supernumerary serrations). Hair tuft of maxilla near base of palp pale, sparse and very inconspicuous. Third antennal segment normally not more strongly pigmented than other parts of antenna. Abdominal cuticle bare or setose. Rectal gills simple or compound. Cephalic apotome with positive or negative spots, broadest near posterior margin (a few exceptions) . . . . . **SIMULIUM** Latreille (p. 34)

## SIMULIINAE Newman

SIMULIITES Newman, 1834, *Ent. Mag.* **2** : 387. Type-genus : *Simulium* Latreille, 1802.

Diagnosis. Lower mesothorax with mesepisternal sulcus, katapisternal region bulbous and clearly delimited. Wing with vein  $R_1$  long and merging with costa in apical half of wing; wing membrane with a crease-like submedian fork between  $M_2$  and  $Cu_1$  (Text-fig. 1), sometimes very weak. Style of male hypopygium with one or more apical spinules.

## PROSIMULIINI Enderlein

PROSIMULIINAE Enderlein, 1921, *Dt. tierärztl. Wschr.* **29** : 199. Type-genus : *Prosimulium* Roubaud, 1906.

HELLICHIINI Enderlein, 1925, *Zool. Anz.* **62** : 203. Type-genus : *Hellichia* Enderlein, 1925.

ECTEMNIINAE Enderlein, 1930, *Arch. klassif. phylogen. Ent.* **1** : 81. Type-genus : *Ectemnia* Enderlein, 1930.

STEGOPTERNINAE Enderlein, 1930, *Arch. klassif. phylogen. Ent.* **1** : 81. Type-genus : *Stegopterna* Enderlein, 1930.

CNESIINAE Enderlein, 1934, *Dt. ent. Z.* **1933** : 273. Type-genus : *Cnesia* Enderlein, 1934.

GYMNOPAIDINAE Rubzov, 1956, *Fauna SSSR* (n.s.), No. 64, *Diptera* **6** (6) : 186. Type-genus : *Gymnopais* Stone, 1949.

CNEPHIINI Grenier & Rageau, 1960, *Bull. Soc. Path. exot.* **53** : 739. Type-genus : *Cnephia* Enderlein, 1921.

Diagnosis. Mesepisternal sulcus broad and often shallow, evanescent anteriorly (Text-figs. 16, 18); katapisternum in profile short and deep (Text-fig. 18). Pedisulcus absent. Costa and other veins sometimes without spiniform macrotrichia. Vein  $R_s$  sometimes forked. Vein  $Cu_2$  sometimes straight or almost so. Basal cell present (Text-fig. 1), almost always distinct, sometimes absent. Last segments of maxillary palp short subcylindrical, subequal in length to third segment. Fore tarsus slender. Basal section of radius always haired. Pleural membrane bare (rarely a few hairs on sclerotized part of upper mesopleuron, very rarely on membrane). ♂ head sometimes dichoptic. Cocoon usually a loosely woven bag without regular or discrete form or well defined anterior edge, rarely almost absent (when reduced to holdfast and a few strands). Pupal abdomen with long strong terminal hooks, if these reduced to pointed or blunt spikes then still conspicuously longer than their basal width. Cuticle of pupal abdomen with thickened sclerotized tergal and sternal plates, often with discretely formed pleural plates or small rounded pleurites, the pale brown sclerotization conspicuous on the cast pupal pelt : venter of abdominal segments 6 and 7 (sometimes also 8) with semi-membranous longitudinally striate area in the mid-line dividing the sternal plates of these segments (inconspicuous in a few forms where the cuticle more delicate than usual). Some of the abdominal segments of the pupa with backwardly directed spine-combs or at least with granulations on transverse ridge-like swellings of the terga. Larva sometimes without cephalic fans. Inner secondary mouthbrush often flat subtriangular with ray tips forming a straight line. Larval head-spots positive (except *Ectemnia*). Cephalic apotome often widest well before hind margin. Larval cervical sclerites often merged in continuous sclerotization with upper end of postoccipt (Text-fig. 20). Larval mandible usually with third comb-tooth enormously enlarged (Text-fig. 55) and mandibular serrations often in long sawlike series (Text-fig. 55) (almost always more than two serrations). Postgenal cleft never reaching hypostomium, usually a small subrectangular notch shorter than postgenal bridge (Text-fig. 45). Hypostomium often trifid with teeth in three main prominent groups. Larval maxilla with conspicuous thick hair tuft near base of palp. Larval cuticle bare. Anal sclerite sometimes Y-shaped or absent. Rectal gills simple trilobed, without secondary lobules.

The tribe Prosimuliini as now defined contains the genera *Gymnopais* Stone, *Twinnia* Stone & Jamnback, *Prosimulium* Roubaud, *Crozelia* Davies, and *Gigantodax* Enderlein, which are widely accepted as full genera. In addition it contains several other genus-group segregates that are variously treated either as full genera or as subgenera by different specialists : these include *Astega* Enderlein, *Cnephia* Enderlein, *Cnesia* Enderlein, *Ectemnia* Enderlein, *Greniera* Doby & David, *Lutzsimulium* d'Andretta & d'Andretta, *Paraustrosimulium* Wygodzinsky & Coscarón, *Paracnephia* Rubzov and *Stegopterna* Enderlein. It is outside the scope of the present work to consider these segregates further, except for *Paracnephia*, since none of them occur in Africa, but a new treatment of them will be presented in a later paper. The only Prosimuliine genus found in Africa is *Prosimulium* Roubaud s.l., in which I include Rubzov's *Paracnephia* as a subgenus, and this genus is treated fully below : the genus *Metacnephia* gen. n. fits Prosimuliini on some of its characters but on balance it has been considered better to assign it to Simuliini, as discussed more fully elsewhere.

### PROSIMULIUM Roubaud

*Prosimulium* Roubaud, 1906 : 521. Type-species : *Simulia hirtipes* Fries, 1824, by subsequent designation of Malloch, 1914 : 16.

Diagnosis. Antennae with 9-12 segments. Head without definite postocular semi-shining bullate area. Scutum not covered with long erect hair. Costa and other veins with or without spiniform macrotrichia as well as hairs. *Rs* forked or simple. Vein *Cu*<sub>2</sub> sinuous with double curvature. Basal cell usually distinct. Calcipala varied, from very strong to completely absent. Basal section of radius with all hair semi-recumbent. ♂ style with single or multiple spinules. Cocoon normally covering pupal body, often incorporating inorganic particles, rarely reduced to cover only part of abdomen or to a few threads. Gill of pupa filamentous or arborescent, sometimes with one or more main trunks from which filaments arise. Pupal abdomen with fully developed onchotaxy, without anchor-like hooklets terminally (except in subgenus *Greniera*). Larval head with cephalic fans (except sometimes in first instar), the fans normal; inner secondary fan with tips of rays forming an arc or rather straight so that inner fan is flat subtriangular. Head with normal shape or strongly convex laterally, cephalic apotome usually broadest well in front of hind margin but sometimes at posterior end. Hypostomium often with trifid apex, but much variation. Antenna short with third segment heavily pigmented or long and pale. Mandibular shape normal, serrations varying from long series to only two or three, third comb-tooth often enormously enlarged compared to others. Cervical sclerites often merged with sclerotized extensions from upper ends of postocciput, but sometimes isolated in neck membrane. Anal sclerite normal X-shaped (except absent in subgenus *Ectemnia*). Ventral papillae normally absent, occasionally present. Last abdominal segment without sclerotized accessory ring.

Distribution. Widespread throughout the Holarctic Regions, including sub-Arctic Baffin Land, Iceland and Bear Island ; also Japan. In the broad sense for the genus here used, distribution includes northern Central America, Patagonia, eastern and southern Africa, and eastern and western mainland of Australia. African distribution as in Map 1.

Discussion. In recent years the name *Prosimulium* has been applied only to a

small number of Simuliids in the fauna of North America and the USSR (where most work has been done) that form a distinctive group recognized by the presence of a fork in vein *Rs*, by lacking the calcipala, and by having the costa and radial veins haired without any development of spiniform macrotrichia, as well as by a number of other rather distinctive features in the immature stages. So long as only the fauna of the Holarctic area is considered these characters hold good for the delimitation of a rather conspicuous and easily characterized genus, but when forms from the whole world fauna are taken into consideration it no longer becomes possible to delimit *Prosimulium* at all clearly by the old characters that worked well for a limited area : for example, forms from southern Africa or from Western Australia, which on overall balance of characters have a completely *Prosimulium*-like facies, simply fail to fit with the old definitions or alternatively to show combinations of characters among themselves that could serve to exclude them satisfactorily from *Prosimulium*. For examples of the difficulties met may be mentioned a species from Australia (*tonnoiri* Drummond) in which vein *Rs* sometimes has a definite fork while at other times it is simple, or a species from Africa (*morotoense* McCrae & Prentice) in which the costal vestiture is hair-like in the female but incipiently spiniform in the male.

It seems to me that it is no longer possible in the interests of a balanced world classification to maintain *Prosimulium* in the old narrow sense favoured by workers in North America, Europe and USSR (and as used for example in the recent publications of Rubzov, 1956, 1959-1964 ; Stone, 1963, 1964, 1965) and I prefer to treat *Prosimulium* in a broad sense but divided into a number of named subgeneric segregates—thus establishing a concept for *Prosimulium* that equates with that accepted by most workers for *Simulium* s.l. and balances the classification of the more primitive forms in segregates more equivalent to those recognized for the more advanced forms. A detailed account of the subgenera of *Prosimulium* s.l. thus recognized on a world basis will be presented later, and here it is only necessary to put forward keys to, and diagnoses of, the three subgenera that occur in Africa (note that *Prosimulium* s.l. in the African area is confined to continental Africa and is absent from the Malagasy Region and the other islands).

The genus is only known from a few scattered African localities, and very little material is yet available in collections from Africa, but future collecting will almost certainly 'fill in' some of the apparent breaks in distribution ; until recently the forms here placed in *Prosimulium* (previously placed in *Cnephia* Enderlein by Freeman & de Meillon (1953)) were believed to be confined to the extreme south of Africa (Cape Province and South-West Africa) but the recent description of species from Uganda by McCrae & Prentice (1965) and from Rhodesia by Crosskey (1968) has shown that there is not nearly such a wide gap in distribution of *Prosimulium*-like forms in the Palaearctic and southern Africa as was previously supposed. Careful collecting in future in areas of outcropping granite massifs and inselbergs (which seem to provide a favoured environment, even if the streams are only intermittently flowing) may link the distribution still more closely to that of the Palaearctic, for there are no reasons at all for supposing that Prosimuliine forms in southern Africa had a southern route of entry : they are more likely remnants

of a widely distributed Prosimuliine fauna common to the Holarctic and Ethiopian areas.

No really satisfactory larval characters have been found on the limited material available for separating the African subgenera in this stage, and furthermore some species have been described only from the adult. The following key to subgenera is therefore based only on adult and pupal characters.

KEY TO THE SUBGENERA OF *PROSIMULIUM* IN AFRICA

- 1 Vein *Rs* forked (Text-fig. 1). Costa with hair-like macrotrichia only. Pupal abdomen on each side of segments 4 and 5 with a large pleural plate isolated from terga and sterna by paired longitudinally striate semi-membranous areas. [Morocco] . . . . . ***PROSIMULIUM*** Roubaud s. str. (p. 19)
- Vein *Rs* not forked, sometimes dilated apically and with vestigial trace of forking. Costa with or without spiniform macrotrichia. Pupal abdomen without large pleural plates on segments 4 and 5, only one main longitudinally striate area between the terga and sterna (Text-fig. 42). [Ethiopian Africa] . . . . . 2
- 2 Costa with hair-like macrotrichia only, at most some slightly stouter setae in male. Calcipala more or less absent (Text-fig. 22). Pupal gill with 6 or 7 filaments intertwining apically (Text-figs. 38, 39) . . . . . ***PROCNEPHIA*** sgen. n. (p. 21)
- Costa with well developed spiniform macrotrichia as well as hair-like macrotrichia. Calcipala moderately to strongly developed (Text-figs. 23–25). Pupal gill with 10–22 filaments (except *brinchi* with 6, but then widely divergent, Text-fig. 41) . . . . . ***PARACNEPHIA*** Rubzov (p. 23)

SYSTEMATIC TREATMENT OF THE SUBGENERA

In the diagnoses that follow only those characters are shown, in the interests of brevity, that are differential between the subgenera occurring in Africa. All three subgenera in Africa share certain characters that differ from those found in some extra-limital subgenera of *Prosimulium*, particularly the following that differentiate from the non-African segregates indicated: style with multiple spinules (distinction from *Cnephia* = *Astega*, *Ectemnia*, some *Greniera*); antenna with 11 segments (distinction from some *Greniera*, also from some extra-limital *Prosimulium* s. str.); more or less complete cocoon present (distinction from *Greniera*); cocoon not stalked (distinction from *Ectemnia*); at least four abdominal segments of the pupa with well developed spine-combs (distinction from *Cnesia*); larval anal sclerite present (distinction from *Ectemnia*); larval abdomen without ventral papillae or transverse ventral fold on last segment (distinction from *Greniera*, *Ectemnia*, *Stegopterna*); larval antenna short, not longer than stem of cephalic fan (distinction from *Stegopterna*, *Greniera*, *Ectemnia*).

Subgenus ***PROSIMULIUM*** Roubaud

*Prosimulium* Roubaud, 1906 : 521. Type-species : *Simulia hirtipes* Fries, 1824, by subsequent designation of Malloch, 1914 : 16.

*Helodon* Enderlein 1921 : 199. Type-species : *Simulia ferruginea* Wahlberg, 1844, by original designation.

- Taeniopterna* Enderlein, 1925 : 203. Type-species : *Melusina macropyga* Lundström, 1911, by original designation.
- Hellichia* Enderlein, 1925 : 203. Type-species : *Hellichia latifrons* Enderlein, 1925, by original designation.
- Mallochella* Enderlein, 1930 : 91. Type-species : *Mallochella sibirica* Enderlein, 1930 [= *Simulia hirtipes* Fries, 1824], by original designation. Junior homonym, preoccupied by *Mallochella* Duda, 1925 (Diptera), see *Mallochianella*.
- Mallochianella* Vargas & Diaz Najera, 1948 : 67. Replacement name for *Mallochella* Enderlein, 1930, preoccupied.
- Urosimulium* Contini, 1963 : 89. Type-species : *Urosimulium stefanii* Contini, 1963 [= *Prosimulium aculeatum* Rivosecchi, 1963], by original designation.

Diagnosis. Costa with hair-like macrotrichia only. Vein *Rs* forked (Text-fig. 1), the fork well before apex but the two branches sometimes lying closely parallel, hair vestiture dividing and running along each branch. Calcipala absent or at most rudimentary. Claws of ♀ simple or with minute pointed basal denticle, rarely with well developed tooth. Gonapophyses of ♀ terminalia usually produced pointed-tonguelike. Pupal abdomen with large lateral pleural plates on segments 4 and 5, these separated from terga and sterna of these segments by paired longitudinally striate areas. Pupal gill in the one North African species with 12 filaments branching near base (variously formed in extra-limital species, often with one or more irregular main trunks from which slender filaments arise). Outermost tooth of each outer group of larval hypostomial teeth almost always longer than, or at least subequal to, other teeth. Larval mandible with irregular saw-like serrations numbering 8–25 (very rare exceptions with only about six serrations).

Distribution. Throughout Holarctic Regions, including Iceland, Japan, Mediterranean islands, North Africa (Morocco) and the Middle East (Lebanon). The distribution includes Bear Island (Björnöya) in the Arctic Ocean, the most northerly known locality for Simuliidae.

Discussion. In Africa the subgenus *Prosimulium* is known only from some localities in Morocco recorded by Grenier *et al.* (1957) for a species identified by them as perhaps the European species *P. (P.) hirtipes* (Fries), but differing in the pupal stage by having the gill with 12 filaments instead of the usual 16; unfortunately Moroccan material consists only of some larvae and one pupa. It is possible that other species exist in North Africa, or that this same species is much more widely distributed; it is not particularly surprising to find *Prosimulium* s. str. in North Africa, as Rivosecchi (1964) has now recorded five species from Sicily and a more or less continuous distribution presumably could have existed at geological periods when the Sicilo-Tunisian land-bridge was broad and complete, or at least such could have provided a route of overland dispersal (furthermore *Prosimulium* s. str. occurs in the Spanish Sierra Nevada which is geographically very close to the areas of the Moroccan Middle Atlas in which *Prosimulium* also occurs).

The segregate *Helodon* Enderlein has been ranked by Stone (1963, 1965) as a subgenus of *Prosimulium* and by Rubzov (1959–1964) even as a full genus. The type-species (*ferrugineum* Wahlberg) appears distinctive because of the reddish colour of the adults and particularly because of the unusual form of pupal gill (see figure 44 in Rubzov, *op. cit.*), but as pointed out by Stone (1963 : 10) the segregate *Helodon* can at best be only very weakly defined; in fact, there appears to be little real distinction between *onychodactylum* Dyar & Shannon, which Stone (1963, 1965)

considers to be the only Nearctic species assignable to *Helodon*, and some North American *Prosimulium* s. str. On a world basis I can see no justification for treating *Helodon* as a valid subgenus, and regard it as forming at most a species-group within *Prosimulium* s. str. equivalent to the *hirtipes*-group as recognized by Rubzov : I therefore place *Helodon* as a synonym of *Prosimulium* s. str.

Likewise the segregate *Urosimulium*, described by Contini (1963) as a full genus, I cannot see as more than a moderately distinctive species-group within *Prosimulium* s. str., and therefore sink the name in synonymy ; Contini cited as diagnostic characters the elongation of the cerci of the female, the triangular shape of the male ventral plate and the bilobate character of the male style, but no differences in the immature stages from *Prosimulium* s. str. More recently Contini (1966) has been obliged, because of the elongate female cerci and bilobate style, to place in *Urosimulium* a second species in which the male ventral plate is quite another shape. The indentation of the style and attenuation of the cerci are matters of degree, and in the absence of clear-cut adult features or of any characters from the early stages for separating *Urosimulium* it is impossible to accept this segregate as valid at subgeneric level if named segregates are to be adequately balanced : like *Helodon*, I consider it best to treat *Urosimulium* as at most a species-group within the subgenus *Prosimulium* s. str., and to sink the former name as a synonym.

The other names cited in synonymy with *Prosimulium* s. str. (see above) have been discussed by Stone (1963), and no further comment on these is required.

Rubzov (1959-1964) recognizes three species-groups in the Palaearctic fauna of *Prosimulium* s. str., but these have not been considered in detail for purposes of the present paper as only the one species, record cited above, is known from Africa ; this belongs in Rubzov's *hirtipes*-group, which is therefore the only group of *Prosimulium* s. str. found in the African area.

Included taxa. All Nearctic species placed in the genus *Prosimulium* in the catalogue of Stone (1965), and all Palaearctic species placed in *Prosimulium* and *Helodon* in the monograph of Rubzov (1959-1964). In addition the following recently described Palaearctic species that are not covered in Rubzov (op. cit.) : *albense* Rivosecchi, 1961 ; *aculeatum* Rivosecchi, 1963 (= *stefanii* Contini, 1963) ; *goidanichi* Rubzov, 1964 ; *juccii* Contini, 1966.

The assignment of all these species to subgenus *Prosimulium* s. str. in an enlarged concept for the genus does not involve new combinations, except for *Urosimulium juccii* Contini for which the new assignment is *Prosimulium* (*Prosimulium*) *juccii* (Contini) **comb. n.**

#### Subgenus *PROCNEPHIA* sgen. n.

Type-species : *Prosimulium rhodesianum* Crosskey, 1968.

Diagnosis. Costa with hair-like macrotrichia only, some macrotrichia in male sometimes thickened and differentiated from hairs but not fully spiniform. Vein *R*<sub>5</sub> not forked, though sometimes slightly expanded apically with suggestion of last remnant of forking. Calcipala absent or very rudimentary (Text-fig. 22). Claws of female with moderately developed to large

tooth. Gonapophyses of ♀ terminalia as in *Paracnephia* (Text-fig. 34). Pupal abdomen without large pleural plates on sides of segments 4 and 5, terga and sterna of these segments separated by a single longitudinally striate area with at most only minute platelets. Pupal gill with six or seven filaments, convergent at the tips. Ventral plate of ♂ flattened, without lip, slender in profile (Text-figs. 26, 27). Style of ♂ curved and excavate on inner side (Text-fig. 31), sometimes longer than coxite. Larval hypostomium with outermost tooth of each outer group always shorter than main tooth of outer group (Text-figs. 49, 50). Larval mandible with irregular saw-like series of about 10–16 serrations, sometimes apparently only a few and very blunt (but this probably due to wear or damage).

Bionomy. [Oviposition habit unknown.] Larvae and pupae attached to rock surfaces or lithophilic mosses in fast water, sometimes in closely aggregated masses, in streams subject to periodical drying; cocoons sometimes very weakly differentiated and pupae in almost common silk network, mature larvae apparently in this case migrating to common pupation ground (de Meillon & Hardy (1951)). [Biting preferences of forms with fully developed female mouthparts unknown; female mouthparts sometimes partially atrophied and presumed non-functional, therefore such forms autogenous.]

Distribution. Known distribution very sparse and scattered (Map 1), recorded from South-West Africa, South Africa, Rhodesia and Uganda.

Discussion. The subgenus *Procnephia* is here erected, with *P. rhodesianum* Crosskey as type-species, for a small number of species that I have elsewhere referred to as the *damarensis*-group (Crosskey, 1968). These species are difficult to place satisfactorily in a classification that looks at world forms since their characters almost completely interlink those of true Holarctic *Prosimulium* with those of *Paracnephia*, a segregate rather weakly defined by Rubzov (1962) that he proposed for the inclusion of all the primitive southern African black-flies previously placed by Freeman & de Meillon (1953) in the genus *Cnephia*. If the intermediate species here constituting the new subgenus *Procnephia* are assigned arbitrarily to either *Prosimulium* or *Paracnephia* it makes the resultant group very difficult to define, and I think it better to treat them as a small subgenus on their own, ranked equivalent to *Paracnephia* and placed in sequence between *Prosimulium* s. str. and *Paracnephia* (in the more restricted sense in which this segregate is now defined). Even so, it cannot be claimed that any of the three subgenera can be entirely satisfactorily delimited, and it is the existence of these "awkward" intermediate forms in Ethiopian Africa (there are others in Australia, southern South America and northern Central America) that convinces me that it is essential to re-define *Prosimulium* more broadly than in the past and to incorporate into it, as subgenera, a range of forms that overlap so closely in their characters with *Prosimulium* in the strict sense that no clear generic distinctions can be maintained.

*Procnephia* has the costa and radial veins entirely hairy as in *Prosimulium* s. str. but has more or less lost the clear bifurcation of *Rs* (assuming as usual that a more complete venation is 'primitive'): even in this character, however, the distinction is not absolute, for some specimens of *Procnephia* (if the wing is carefully examined) show clear traces of doubling at the extreme tip of *Rs* and may show a parting into two irregular rows of the hair vestiture, which may fairly be interpreted as the last

vestigial remnant of a fork. The almost completely undeveloped calcipala is also similar to that of *Prosimulium* s. str. but the immature stages of *Procnephia* (in which the pupa has lost the large pleural plates of the intermediate segments of the abdomen and the larval hypostomium has the outermost tooth relatively small) are not really separable from those of *Paracnephia*. The male hypopygium differs slightly, but apparently consistently, between *Procnephia* and *Paracnephia* as the ventral plate in the former is always rather flattened with a slender slightly curved profile (Text-fig. 27), whereas in the latter the shape in profile, although diverse, is always more expanded (Text-figs. 29, 30) : likewise the style in *Procnephia* is excavate and markedly concave on the inner surface, whereas in *Paracnephia* there is no such excavation (Text-figs. 32, 33). In the pupa the six or seven-filamented gill, with the intertwining tips of the filaments, is distinctive in *Procnephia*, although one species (*brincki*) of *Paracnephia* also has a gill of six filaments (though differently disposed, since they diverge widely).

Included taxa. *Prosimulium* (*Procnephia*) *damarensis* de Meillon & Hardy ; *P.(P.) morotoense* (McCrae & Prentice) ; *P.(P.) rhodesianum* Crosskey.

#### Subgenus *PARACNEPHIA* Rubzov stat. n.

*Paracnephia* Rubzov, 1962 : 1491. Type-species : *Cnephia muspratti* Freeman & de Meillon, 1953, by original designation.

Diagnosis. Costa with well formed spiniform macrotrichia intermixed with hair-like macrotrichia. Vein Rs not forked. Calcipala present, small to well formed (Text-figs. 23-25). Claws of ♀ with well developed basal tooth. Gonapophyses of ♀ terminalia rounded-lobate (Text-fig. 34). Ventral plate of ♂ widened apically in profile (Text-figs. 29, 30), in ventral view usually appearing slightly 'lipped' (Text-fig. 28). Style of ♀ not concavely excavate on inner side (Text-figs. 32, 33). Pupal gill with 10-22 filaments (except 6 in *brincki*). Pupal abdomen without large pleural plates on segments 4 and 5, terga and sterna of these segments separated by a single longitudinally striate area which at most is interrupted only by minute platelet-like spaces [but see discussion]. Larval hypostomium with outermost tooth of each outer group of teeth shorter than the main tooth of the outer group (Text-figs. 51-53). Larval mandible with saw-like series, usually about 12 in number, of mandibular serrations, these most often on rather expanded flange.

Bionomy. So far as known, as for *Procnephia* (see above).

Distribution. South-West Africa and South Africa (Map 1), but very similar forms, possibly consubgeneric, present in Australia and Central America.

Discussion. The subgenus *Paracnephia*, as here re-defined in subgeneric status within the genus *Prosimulium* s.l., contains all the forms (except *damarensis*) that were placed in *Cnephia* by Freeman & de Meillon (1953) and in the genus *Paracnephia* by Rubzov (1962), together with the species described in *Cnephia* by de Meillon (1955). Although the included species are slightly diverse, and two (*turneri* and *herero*) are still known only from the female holotypes, they are sufficiently uniform in their main characters to allow of a reasonably firm definition of the

segregate ; but it should be emphasised that the diagnosis may require amendment when the other stages of *herero* or *turneri* become known, or when further species are discovered (as seems likely when the habitats favoured by Ethiopian *Prosimulium* s.l. species are more thoroughly investigated). Furthermore, I think it almost certain that when the characters of Australian *Prosimulium*-like forms, and possibly also those of Mexico and Guatemala, are studied in detail it will be found necessary to bring these species into the subgenus *Paracnephia*, when a widening of the definition of the concept may be needed (as, for example, the larvae of some Central American forms possess ventral papillae, and the pupa of at least one Australian species has large lateral pleural plates on the abdomen).

Some species of *Paracnephia* have fully toothed mandibles and maxillae in the female and are presumably biting forms that may be anautogenous ; these have from 10–15 outer teeth and 24–35 inner teeth on the mandible, and from 10–15 outer teeth and from 16–18 inner teeth on the maxilla, and include *turneri*, *brincki* and *thornei*. Other species have the apices of the female mandibles and maxillae atrophied, without definite teeth but with a jagged margin on the mandibles and with haired apex on the maxillae : these forms presumably cannot bite and are autogenous ; they include the type-species, *muspratti*, and also *harrisoni* and *barnardi*. The condition of the female mouthparts in *herero* is unknown (it is undesirable to break up the head of the unique holotype until this should prove essential). The condition of the female mouthparts does not correlate in any obvious way with other characters, so that there is evidently no natural species-grouping solely on this character, but the species of *Paracnephia* are here treated in three groups using other criteria (which may not necessarily hold up as satisfactory characters for delimiting groups when more becomes known of this poorly collected and represented subgenus). The three groups are :—

***brincki*-group.** Vein  $R_1$  with hair-like setae only. Calcipala small, similar to *muspratti*-group. Pupal gill with 6 divergent filaments (Text-fig. 41). Fourth abdominal segment of pupa ventrally with only one hook on each side. Terminal hooks of pupa relatively short and spike-like (Text-fig. 44), not sinuous.

Included taxon. *Prosimulium* (*Paracnephia*) *brincki* (de Meillon) **comb. n.**

***muspratti*-group.** Vein  $R_1$  with hair-like setae only. Calcipala small or of medium size (Text-figs. 23, 24). Pupal gill with 10–22 filaments (of type shown in Text-fig. 40). Fourth abdominal segment of pupa with two hooks each side ventrally. Terminal hooks of pupa not at all reduced, long and slightly sinuous (Text-figs. 42, 43).

Included taxa. *Prosimulium* (*Paracnephia*) *barnardi* (Gibbins) **comb. n.** ; *P.(P.) harrisoni* (Freeman & de Meillon) **comb. n.** ; *P.(P.) herero* (Enderlein) **comb. n.** ; *P.(P.) muspratti* (Freeman & de Meillon) **comb. n.** ; *P.(P.) thornei* (de Meillon) **comb. n.**

***turneri*-group.** Vein  $R_1$  with spiniform as well as hair-like setae (similar to *costa*). Calcipala large and of the *Simulium* type (Text-fig. 25). [Pupal characters unknown.]

Included taxon. *Prosimulium* (*Paracnephia*) *turneri* (Gibbins) **comb. n.**

## SIMULIINI Newman

SIMULIITES Newman, 1834, *Ent. Mag.* **2** : 387. Type-genus : *Simulium* Latreille, 1802.

NEVERMANNIINI Enderlein, 1921, *Dt. tierärztl. Wschr.* **29** : 199. Type-genus : *Nevermannia* Enderlein, 1921.

FRIESIINI Enderlein, 1936, *Sber. Ges. naturf. Freunde Berl.* **1936** : 117. Type-genus : *Friesia* Enderlein, 1922.

WILHELMIINI Enderlein, 1936, *Sber. Ges. naturf. Freunde Berl.* **1936** : 119. Type-genus : *Wilhelmia* Enderlein, 1921.

ODAGMIINI Enderlein, 1936, *Sber. Ges. naturf. Freunde Berl.* **1936** : 127. Type-genus : *Odagnia* Enderlein, 1921.

AUSTROSIMULIINI Smart, 1945, *Trans. R. ent. Soc. Lond.* (B) **95** : 472. Type-genus : *Austrosimulium* Tonnoir, 1925.

Diagnosis. Mesepisternal sulcus deep, well defined, usually very narrow and more or less complete anteriorly (Text-figs. 17, 19) ; katepisternum in profile almost always distinctly longer than its depth (Text-fig. 19). Pedisulcus present or absent. Costa with spiniform macrotrichia intermixed with hair-like setae. Vein *Rs* always undivided, *Cu*<sub>2</sub> always sinuous with double curvature. Basal cell absent or present. Last segment of maxillary palp slender and tapering, much longer than either of the two preceding segments (some exceptions). Fore tarsus slender or dilated. Basal section of radius haired or bare. Pleural membrane bare or haired. ♂ head always holoptic. Cocoon discrete and well formed (even if reduced to cover only pupal abdomen), simple or shoe-shaped. Pupal abdomen with small terminal tubercles, blunt or at most slightly thorn-like. Cuticle of pupal abdomen pale and membranous without definite brown sclerotized terga or sterna and without pleural plates, abdomen without longitudinally striate areas on the mid-venter of segments 6-8, cuticle mainly forming a delicate transparent pellicle in cast pelt. Pupal abdominal segments 6-8 with or without backwardly-directed spine-combs. Larva always with cephalic fans, tips of inner fan rays forming arc. Larval head pattern varied; cervical sclerites of mature larva always completely isolated in neck membrane from upper ends of postocciput (Text-fig. 21); cephalic apotome widest near hind margin (a few exceptions). Larval mandible with third comb-tooth not enormously enlarged, inner edge of mandible never with long saw-like series of serrations (serrations at most numbering 4-5, usually two). Post-genal cleft very varied but sometimes reaching base of hypostomium. Hypostomium usually with nine apical teeth in rather even row, without teeth aggregated in three main prominent groups (but variant forms occur). Larval maxilla with hair tuft near base of palp sparse, pale and inconspicuous. Larval cuticle bare or with setae of varied forms. Anal sclerite X-shaped, always present. Rectal gills often with secondary lobules.

The tribe Simuliini as here defined contains four genera : the very large cosmopolitan genus *Simulium* Latreille in the broad sense, the endemic Australasian genus *Austrosimulium* Tonnoir (occurring in Australia, Tasmania, New Zealand and Campbell Island), the new monotypic genus *Afrosimulium* gen. n. from southern Africa, and the Holarctic genus *Metacnephia* gen. n. here described for most of the species previously placed in '*Cnephia*' of authors (not of Enderlein). The differences between *Simulium*, *Afrosimulium* and *Metacnephia* are indicated in the accompanying keys, diagnoses and discussion sections later in this paper, but a few of the main characters of the extra-limital genus *Austrosimulium* may be enumerated here to indicate how this genus differs from the Simuliine genera occurring in Africa.

In *Austrosimulium* the antennae are 10-segmented (rarely even with only 9 segments) instead of 11-segmented as in the other genera (some very rare exceptions occur in *Simulium* in which the antenna has 10 or 12 segments), and the male style has multiple spinules (almost always one spinule in the other genera, although a few

*Simulium* have more than one) ; the X-shaped sclerite of larval abdomen has a backwardly-directed strut from each anterior arm in *Austrosimulium* which is absent in other genera of Simuliini, and many forms show a ring-like accessory sclerotization around the last larval abdominal segment which is also normally absent in the other genera (though traces of such annular sclerotization are found in some *Simulium* larvae from Madagascar and New Guinea). *Austrosimulium* pupae lack dorsal spine-combs on the terminal abdominal segments like the pupa of *Afrosimulium* and some *Simulium* but usually have some multiramous hooklets similar to those of *Metacnephia*. The adult of *Austrosimulium* resembles *Simulium* very closely in having both well developed calcipala and pedisulcus (both of these features are virtually absent in *Metacnephia* and only the pedisulcus is well developed in *Afrosimulium*) ; the wing has hair-like setae only on the apical part of  $R_1$  whereas in *Simulium* vein  $R_1$  almost always has some spiniform setae in addition (but not in subgenus *Hebridosisimulium* Grenier & Rageau from the New Hebrides in which  $R_1$  has hairs only). The rectal gills of the *Austrosimulium* larva are always simple, whereas they are very often compound, with numerous finger-like secondary lobules in *Simulium* larvae. Taking all characters together, *Austrosimulium* may be accepted as a valid genus, although certainly very close to *Simulium* Latreille s.l.

#### **METACNEPHIA gen. n.**

Type-species : *Cnephia saileri* Stone, 1962.

Genus of uncertain position, tentatively assigned to Simuliini and showing following combination of characters :

Diagnosis: ♂♀. Antenna with 11 segments. Head and eyes normal. Pleural membrane usually haired [as in type-species], sometimes bare. Mesepisternal sulcus deep but sometimes widened, almost complete anteriorly. Katepisternum bare. Costa with spiniform and hair-like macrotrichia. Vein  $R_s$  simple,  $Cu_2$  sinuous. Basal cell present. Basal section of radius haired. Wing membrane with normal microtrichia. Fore tarsus slender. Calcipala absent or minute. Pedisulcus absent. ♂ : hypopygium with simple tapering or slightly truncate styles, style with one apical spinule; ventral plate lamellate, haired, transverse or subtriangular; parameral hooks numerous; median sclerite elongate and cleft apically. ♀ : cibarium unarmed. Claws with large basal tooth. Gonapophyses simple, bluntly rounded or truncate lobes. *Pupa* : Gill arborescent, 13–150 filaments with branching usually in basal half of gill, when fine filaments very numerous these sometimes arising from a few large bulbous trunks. Abdominal cuticle largely pale, delicate and membranous, cast pelt of pupa therefore without conspicuous brownish sclerites ; no differentiated pleural plates, or conspicuous longitudinally striate areas. Last segment with pair of small blunt terminal tubercles. Eighth and ninth (sometimes only the last, ninth) abdominal segments laterally with grapnel-like or anchor-like divided hooklets (Text-fig. 35). Abdominal segments 7 and 8 (sometimes also 6 or 5 and 6) with backwardly-directed spine-combs. Normal basic abdominal onchotaxy (i.e. four hooks each side dorsally on segments 3 and 4, two close-set hooks each side ventrally on segment 5 and two widely spaced hooks ventrally each side on segments 6 and 7) supplemented by additional spinous, often recurved, setae on some or most segments, including transverse row dorsally on segment 2 (sometimes also segment 1), extra setae outside main hooks dorsally on 3 and 4, some setae ventrally on segments 3 and 4 (sometimes also 2), and sometimes extra ventral setae on segment 5, occasionally other slight variants. Cocoon shoe-shaped, form discrete and neck often well raised from sub-

strate, covering pupal body and often entirely concealing gills. *Larva* : Head not noticeably convex, cephalic fans present and normal. Cephalic apotome broadest near hind margin or slightly forward. Head-spots positive or pigmentation pattern not definitely classifiable. Postgenal cleft large and elongate, almost subparallel-sided or tapering anteriorly and broadly reaching base of hypostomium, postgenal bridge therefore widely incomplete (Text-fig. 36). Hypostomium characteristic (Text-fig. 37), apical teeth very reduced and inconspicuous, anterior corners of hypostomium unusually rounded. Mandible with three or four mandibular serrations that form together an expanded serrate flange on inner edge of mandible. Cuticle bare. Ventral papillae absent and last abdominal segment without sclerotized accessory ring. Anal sclerite normal. Rectal gills simple.

**Distribution.** Nearctic Region (mainly from Manitoba to Alaska and in western United States) and Palaearctic Region (from western Europe and North Africa to eastern USSR, including northern Iran).

**Discussion.** The Simuliid fauna of North Africa (Morocco : see Grenier *et al.*, 1957) contains two of the species that belong in the taxonomically troublesome miscellany of forms that have up to now been assigned to the genus *Cnephia*, despite the fact that many of them share few characters in common with those of *Cnephia pecuarum* (Riley), the type-species of *Cnephia*, from the Mississippi. Consideration of the characters shown by the species known from Morocco (*blanci* Grenier & Theodorides and *tredecimatum* Edwards), while preparing the present revision of African Simuliidae, showed that although they obviously fitted exactly into Rubzov's (1959-1964) *pallipes*-group of *Cnephia* this group as a whole was very disjunct in its characters from those of the true *Cnephia* as shown by the type-species, and that the genus '*Cnephia*' as treated by Rubzov or the subgenus '*Cnephia*' in the sense of Stone (1965 : 184) contains an admixture of forms that fall clearly into two quite separate categories. The two facies are so clear cut that it is difficult to accept that there is any close relationship between the segregates, and—equating the combinations of characters with those shown by other genus-group segregates in the Simuliidae—I do not think it possible to treat both as consubgeneric or even as congeneric as recent authors have done without bringing in to the same named segregate forms that are (I believe it fair to judge) clearly polyphyletic. The degree of difference found in the two groups of '*Cnephia*' auct. may be gauged from the following tabulation of the characters involved :

- A. Mesepisternal sulcus wide and shallow, evanescent anteriorly, katepisternum as deep as its length in profile. Last segment of maxillary palp subcylindrical, short and usually subequal to third segment. Pleural membrane bare. Female gonapophyses slightly but distinctly produced tongue-like. Pupal abdomen with long strong terminal hooks and without biramous or trifurcate anchor-like or grapnel-like hooks. Cocoon feeble, usually irregular bag-like without well defined anterior rim. Larval head with postgenal bridge complete, broad, postgenal cleft subequal in length to or shorter than postgenal bridge.
- B. Mesepisternal sulcus sharply defined, deep though sometimes wide, almost complete anteriorly, katepisternum in profile longer than its depth. Last segment of maxillary palp elongate, almost always much longer than third segment. Pleural membrane haired (a few exceptions). Female gonapophyses bluntly truncate. Pupal abdomen without long terminal hooks (with pair of small blunt tubercles), and with complex

anchor-like or grapnel-like hooklets on each side of terminal segments. Cocoon well formed, with discrete definite shape and usually a well defined anterior rim. Larval head with incomplete postgenal bridge, a long postgenal cleft extending forwards to reach the hypostomium.

The type-species of *Cnephia* has facies A delimited above, and so also does *lapponica* Enderlein, the type-species of *Astega* Enderlein, which Rubzov (1959–1964) places in his *lapponica*-group of *Cnephia*. Hence the name *Cnephia* strictly applies to this segregate and *Astega* is a synonym of *Cnephia*.

Forms with the second facies B delimited above, it is here considered, cannot be assigned to the same genus or subgenus as those with facies A, and therefore cannot be placed in *Cnephia*: there is no available genus-group name already published that can be applied to the group, and the new genus *Metacnephia* is therefore here erected for them, with *Cnephia saileri* Stone fixed as type-species (this species has been chosen as type because more material is available than for the other included species). The new genus includes all the taxa assigned to the *pallipes*-group by Rubzov and six of the species listed in subgenus *Cnephia* by Stone (1965): a complete enumeration of the assigned species, establishing the new combinations that arise, is given later.

*Metacnephia* has a suite of characters intermediate between those of *Prosimulium* s.l. and those of *Simulium* s.l., and is therefore an annectant genus between typical forms of Prosimuliini and Simuliini, tending to bridge such character break—at best a rather weakly defined one—that exists between these tribes. Some of the characters of *Metacnephia* are almost unique to the genus or of very rare occurrence elsewhere among world Simuliidae: the larval head-capsule is broadly membranous in the mid-ventral line without a sclerotized postgenal bridge interposed between the usual cleft and the hypostomium (i.e. the postgenal cleft reaches forward on the head capsule to abut broadly on to the base of the hypostomium, thus completely separating the sclerotized genal regions of the two sides of the head as shown in Text-fig. 36); such a head never occurs in the larvae of Prosimuliini (in which the floor of the head-capsule is fully sclerotized for a long distance behind the hypostomium), but there are a few forms of Simuliini in which the cleft reaches forward to the hypostomium (in the subgenera *Byssodon* and *Simulium* s. str. of *Simulium*)—hence the larval head suggests closer affinity with Simuliini than with Prosimuliini. No clear evidence of affinity, however, is suggested by the extraordinary ramified (usually biramous anchor-like or triramous grapnel-like) hooklets at the end of the pupal abdomen in *Metacnephia*, for these are of sporadic occurrence elsewhere, e.g. in at least some species of *Gigantodax* Enderlein (Prosimuliini) and *Austrosimulium* Tonnoir (Simuliini), and in the type-species of the anomalous (at present monotypic) segregates *Greniera* Doby & David from western Europe and *Paraustrosimulium* Wygodzinsky & Coscarón from Tierra del Fuego. The reduced terminal tubercles of the pupal abdomen and the well formed cocoon are of the type found in Simuliini.

The adult stage of *Metacnephia* resembles Prosimuliini because of the lack of pedisulcus and presence of a basal cell in the wing, but the nature of the mesepisternal sulcus and katapisternum (which I believe provides a fundamental distinction

between the more advanced Simuliini and the more generalized Prosimuliini) come much closer to the Simuliine type than to the Prosimuliine type, although slightly intermediate : the sulcus is sharply defined laterally, deep though rather wide, and is almost complete anteriorly, and the katapisternum in side view is normally distinctly longer than its depth. This character therefore fits Simuliini rather than Prosimuliini. Other characters tending towards Simuliini are shown by the maxillary palp (in which the last segment is elongate and as a rule much longer than the third segment, as in *Simulium* s.l.), and by the pleural membrane : in almost all species of *Metacnephia* the pleural membrane is conspicuously haired as in many *Simulium*, whereas (to the best of my knowledge) the pleural membrane is bare in all Prosimuliini—though here it should be noted that some specimens of *Gymnopsis dichopticus* Stone may show a very few strange stiff black setulae on the membrane, and there are a few hairs on the upper sclerotized part of the mesopleuron (just below the scutal ridge) in *Prosimulium morotoense* (McCrae & Prentice).

The balance of characters in *Metacnephia* taken together make it best to assign the genus to Simuliini, a course which seems particularly proper when the *ovtshinnikovi*-group is taken into consideration, for this little known aggregate of species from Transcaucasia, Soviet Central Asia and Siberia has a combination of characters some of which are those of *Metacnephia* and others of *Simulium* s.l. (Rubzov, 1959–1964, defines the *ovtshinnikovi* species-group and places it in *Cnephia*). The *ovtshinnikovi*-group has a well developed and deep pedisulcus, has the pleural membrane bare, sometimes has the katapisternum haired, lacks a definite basal cell in the wing, and has the pupal abdomen without complex anchor-like hooklets and in all of these characters differs considerably from *Metacnephia* ; on the other hand the larval stage is not distinguishable from that of *Metacnephia* and has, for instance, the same type of elongate postgenal cleft, similar hypostomium and mandibular serrations. Since the adult and pupal stages are not adequately separable from *Simulium* s.l., it is considered that the *ovtshinnikovi*-group would be better assigned to this genus, and the group is therefore excluded from *Metacnephia* as here defined : in my view, it has no close affinity at all with the true *Cnephia* Enderlein (even less than *Metacnephia*) and Rubzov's assignment of the group to this genus-group name is inapt.

The species of *Metacnephia* almost all have the pleural membrane thickly haired, but there are a few species in which it is apparently naturally bare : it is haired in all North American species except *M. saskatchewanana* (Shewell & Fredeen) (this species has not been seen but the original description states 'mesopleural membrane bare'), and the majority of Palaearctic species, but not in *M. persica* (Rubzov) ; although Rubzov (1959–1964 : 212) places *persica* in his key-isolate 9 (42) in which the pleural membrane is stated to be haired ('Membran behaart'), his own original description of this species (Rubzov, 1940 : 495) states that the membrane is bare, and this has been confirmed from material seen.

The species assigned here to *Metacnephia* are moderately homogenous and the genus is not divided into species-groups. One included species, *M. pedipupalis* (Rubzov), is atypical however in the characters of the cocoon and does not conform

to the generic diagnosis given : in *pedipupalis* the cocoon has a short stalk and covers only the pupal abdomen, being rather goblet-shaped instead of the normal boot shape.

Included taxa. The following described species are assigned to *Metacnephia* gen. n. and new combinations therefore established :

Nearctic Region : *Metacnephia freytagi* (DeFoliart & Peterson) **comb. n.** ; *M. jeanae* (DeFoliart & Peterson) **comb. n.** ; *M. saileri* (Stone) **comb. n.** ; *M. saskatchewanana* (Shewell & Fredeen) **comb. n.** ; *M. somnermanae* (Stone) **comb. n.** ; *M. villosa* (DeFoliart & Peterson) **comb. n.**

Palaeartic Region : *Metacnephia bilineata* (Rubzov) **comb. n.** ; *M. blanci* (Grenier & Theodorides) **comb. n.** ; *M. crassifistula* (Rubzov) **comb. n.** ; *M. danubica* (Rubzov) **comb. n.** ; *M. edwardsiana* (Rubzov) **comb. n.** ; *M. fuscipes* (Fries) **comb. n.** ; *M. gorodkovi* (Rubzov) **comb. n.** ; *M. hajotsdzorensis* (Terterjan) **comb. n.** ; *M. kirjanovae* (Rubzov) **comb. n.** ; *M. korsakovi* (Rubzov) **comb. n.** ; *M. lesnei* (Séguy) **comb. n.** ; *M. lyrata* (Rubzov) **comb. n.** ; *M. multifilis* (Rubzov) **comb. n.** ; *M. nigra* (Rubzov) **comb. n.** ; *M. octodecimfiliata* (Rubzov & Violovich) **comb. n.** ; *M. pallipes* (Fries) **comb. n.** ; *M. pedipupalis* (Rubzov) **comb. n.** ; *M. persica* (Rubzov) **comb. n.** ; *M. ramificata* (Rubzov) **comb. n.** ; *M. sardoa* (Rivosecchi & Contini) **comb. n.** ; *M. tabescentifrons* (Enderlein) **comb. n.** ; *M. terterjani* (Rubzov) **comb. n.** ; *M. tetraginata* (Rubzov) **comb. n.** ; *M. tredecimata* (Edwards) **comb. n.** ; *M. trigonia* (Lundström) **comb. n.** [*nigra* and *persica* as given include the infraspecific named forms included under these names by Rubzov (1959-1964)].

Two of the Palaeartic species in the foregoing list occur in North Africa, both being recorded from Morocco (Grenier *et al.*, 1957) : they are *Metacnephia blanci* and *M. tredecimata*.

### AFROSIMULIUM gen. n.

Type-species : *Simulium gariepense* de Meillon, 1953.

Genus of Simuliini closely allied to *Simulium* Latreille s.l., with the following combination of characters :

Diagnosis. ♂♀ : Antenna with 11 segments. Head extraordinary [see detailed discussion], not wider than its height, occipital foramen subovate, postgenal lobes not strongly angulate at lower margin of foramen, postgenal membrane wide and area between cardines completely membranous; eye shape modified in accordance with head shape. Last segment of maxillary palp short, subequal to third segment (Text-fig. 305). Pleural membrane bare. Mesepisternal sulcus narrow and deep, sharply defined and complete. Katepisternum bare, longer than its depth in profile. Costa with spiniform and hair-like macrotrichia. Vein *Rs* simple, *Cu*<sub>2</sub> sinuous, submedian fork very indefinite. Basal cell absent or vestigial. Basal section of radius bare. Wing membrane with exceptionally reduced microtrichia (Plate 1B), appearing totally bare hyaline at magnification up to ×100 or ×150. Fore legs exceptionally slender (Text-fig. 307). Calcipala almost absent (Text-fig. 306). Pedisulcus present, deep. ♂ : hypopygium (Text-fig. 308) with small truncate styles with one apical spinule; ventral plate bilobate with each side only narrowly connected medially, basal arms very slender; parameral hooks numerous. ♀ :

cibarium unarmed ; proboscis elongate, subequal to head-height. Claws with large basal tooth. Gonapophyses simple rounded lobes. *Pupa* : Gill trifold, with long subequal tapering branches (Text-fig. 223). Abdominal cuticle membranous and pale, cast pelt of pupa without brownish sclerites (except for usual thickening on last segment). Terminal tubercles small, slightly thorn-like. Abdominal onchotaxy normal (i.e. as usual basic plan in *Simulium*) ; all segments dorsally without spine-combs. Cocoon delicate but discretely formed, shoe-shaped with simple well defined anterodorsal rim, body of cocoon incorporating numerous small inorganic particles. [Larva unknown.]

Distribution. Known only from southern tip of African continent (Map II), in South Africa and Botswana (Bechuanaland).

Discussion. *Afrosimulium* gen. n. is here erected for the single species *gariépense* which de Meillon (1953), in the original description, suggested was probably closely allied to *Simulium griseicolle* Becker because of the bare base to the radius, and presumably because of several other striking resemblances which, although not strongly emphasized by de Meillon, it shares with *griseicolle* : these include the very small size, fine dark lines of the female scutum, rather thick silvery vestiture of the female, large claw-tooth, some resemblance in male hypopygium, and almost identical pupa (the larva of *gariépense* is regrettably still unknown so that comparison of this stage cannot be made). At first, these resemblances suggest convincing evidence for postulating close affinity of *gariépense* with *griseicolle*, and therefore that *gariépense* might be assignable to the subgenus *Byssodon* (syn. *Psilocnetha*) of *Simulium* s.l., but a consideration of all the very extraordinary characters shown by *gariépense* (and not mentioned by de Meillon) shows that the adult stage differs so much from *Simulium* that assignment to this genus (even in its broadest sense) may not be justified. It is necessary to discuss these characters in detail.

The wings of *gariépense* when examined under the entomological microscope, i.e. at magnifications up to  $\times 100$  or  $\times 150$ , appear totally hyaline and bare instead of showing the normal close speckling of dark microtrichia covering the wing membrane ; *gariépense* therefore appears different (at these low magnifications) from all other world Simuliidae, in which the microtrichial vestiture of the wing membrane is obvious. The wings of *gariépense* are in fact closely covered, over the whole membrane surface, with microtrichia but these are exceptionally minute (and also rather blunt and twisted) as compared to those of other black-flies. The difference in size between the normal microtrichia and the reduced microtrichia of *gariépense* is shown by Plate 1A & B, which are photographs at an approximate magnification of  $\times 40,000$  taken by stereoscan microscope, of a part of the mid-wing microtrichial vestiture in (A) *Simulium damnosum* with normal fully developed microtrichia, and (B) *Afrosimulium gariépense* with the very reduced microtrichia. *A. gariépense* is the only known Simuliid in which such vestigial microtrichia occur.

By itself it would be inappropriate to attach much taxonomic significance to the microtrichial reduction, which is a difference of degree rather than kind from other black-flies, but *gariépense* also shows in the head of both sexes a form of sclerotic architecture so completely different from that of all *Simulium* s.l. and almost all other Simuliidae (there is a slight resemblance in the form of the occipital foramen to some *Gymnopais*) that I consider it appropriate to place it in a genus of its own :

if it is placed in an existing named genus this would involve aggregating forms in which the whole fundamental morphology of the adult head-capsule is quite different.

Up to now the form of the head has been little used in the taxonomy of Simuliidae since it offers few characters, and the morphology of the posterior surface of the head has not been studied from the taxonomic viewpoint. Before considering the exceptional features shown by the head of *Afrosimulium* it is therefore necessary briefly to consider the adult head morphology in other black-flies, which are typified by the genus *Simulium* sensu lato (the head of other genera, *Prosimulium*, *Twinnia*, *Gigantodax*, *Austrosimulium* is essentially similar to that of *Simulium* with approximated postgenal lobes and at least weak sclerotization between the cardines but the occipital foramen in these genera tends to be more ovate in the vertical axis than in *Simulium*).

The head-capsule of *Simulium* in facial view is broader than its height in both sexes (Text-figs. 61, 63), and the broad shape with convex outer margins is very evident in posterior view also (Text-figs. 57, 59) ; in profile the head of the male has the eyes rather distinctly subtriangular in general form (Text-fig. 65) with the area of enlarged upper eye-facets at least as long as its height ; the female head in side view, even if the eyes are relatively reduced as in some forms, usually shows no definite angulation of the eye-margin posterodorsally (Text-figs. 66, 69), and the head-height is usually only about a third greater than its length. The morphology of the posterior surface of the *Simulium* head is very constant, only varying throughout the genus by minor differences in degree of sclerotization and by very minor differences in the proportions of certain areas : the occipital foramen is approximately as wide as its height or only very little longer in the vertical than the horizontal axis (Text-figs. 57, 59) ; well sclerotized postgenal lobes have well formed upper inner corners and mainly close the lower end of the foramen, and are only narrowly separated by the postgenal membrane in the mid-line ; the cardines are well visible in posterior view and the area between them is at least weakly sclerotized, so that they are never separated by a wide membranous area (the postgenal membrane therefore does not reach as far as the posteroventral edge of the head (Text-figs. 57, 59)).

In *Afrosimulium* the head-capsule of both sexes in facial view (Text-figs. 62, 64) is not wider than its height, and the relatively narrow shape and less strongly convex eyes are well seen in posterior view (Text-figs. 58, 60) ; in profile the head of the male has the eyes of an inverted pear-shape (Text-fig. 67) with the area of large upper eye-facets higher than long ; the female head in side view is about two-thirds higher than its length and has the hind margin of the eye distinctly angulate near the top (as indicated by the arrow in Text-fig. 68). The posterior surface of the head in *Afrosimulium garipeense* is completely different from that described above for *Simulium* : the occipital foramen is sub-ovate in the vertical axis with the height conspicuously more than the width, and the foramen is closed ventrally only by the exceptionally wide postgenal membrane ; the postgenal lobes are large, very widely separated by the broad unsclerotized postgenal membrane, and have no well formed upper angle against the occipital foramen (Text-figs. 58, 60) ; the cardines lie in a

horizontal plane and are hardly visible from posterior view of the head, the area between them being widely membranous since the broad postgenal membrane area extends ventrally as far as the ventral posterior edge of the head.

The male head in *Afrosimulium* is exceptionally large in relation to body size, and the relatively small occipital foramen is far removed from the top margin of the head-capsule so that the occipital depression (between the foramen and the junction of the holoptic eyes) is very deep (Text-fig. 58) ; on the other hand, the foramen of the female head-capsule is centred above the mid-point of the head (Text-fig. 60). In *Simulium* the occipital foramen of both sexes is situated in the centre of the posterior surface of the head, and the occipital depression of the male between foramen and eye-junction is much wider than its depth (Text-fig. 57).

The head-capsule morphology is so homogeneous throughout the family Simuliidae that the strikingly different adult head architecture found in *Afrosimulium gariépense*—quite unlike that of any other black-fly—is of outstanding interest, for it suggests the possibility that the radical modification of head morphology is associated with some unique biological purpose (at present nothing is known of the behaviour of *gariépense* except that females will hover around man and livestock without biting and that males may come to light). Here it is of interest to note that the whole female proboscis of *gariépense* is much longer than is usual in Simuliids (though not unlike the unusually long proboscis of *Simulium rostratum* Smart & Clifford from New Guinea) and this may be functionally related to the horizontal plane of the cardines and to the other modifications of the lower posterior part of the head : the mouthparts themselves are normal for biting forms, and the possibility exists that elongation of the proboscis (and changes of head morphology, if correlated) are adaptations for feeding on an unusual host. There is no evident explanation for megacephaly of the male.

The calcipala in *A. gariépense* is a very small inconspicuous lobe (Text-fig. 306), described in the diagnosis above for brevity as 'almost absent'; de Meillon (1953) stated that it is absent, but there is clearly some development of a calcipala but not like that of *Simulium* s.l. (although even among *Simulium* there are some forms, such as the Neotropical Andean subgenus *Pternaspatha* Enderlein, in which the calcipala is completely undeveloped). Three other characters may be briefly mentioned : the last segment of the maxillary palp (Text-fig. 305) is short and sub-cylindrical or slightly clubbed, about subequal in length to either the third or fourth segments, and therefore differs from that of *Simulium* in which the last segment is (with very rare exceptions) much longer than either of the two preceding segments and usually tapering and sinuous. The fore leg is unusually slender, with the basitarsus 9–10 times as long as its greatest width and with the tibia thinner than normal (Text-fig. 307). The genital fork of the female terminalia is without the slender forward thumb-like process on each arm that occurs in the superficially similar females of *Simulium* subgenus *Byssodon*.

Finally in this discussion of the characters of *gariépense* it should be emphasized that the new genus *Afrosimulium* is erected for this species with some doubts as to whether this is the most appropriate taxonomic treatment or not. Much depends

upon the importance to be attached to the exceptional head and wing characters, which make *gariépense* difficult to assign satisfactorily to any of the existing genera: if it is not placed in a new genus then it would have to be assigned to *Simulium*, and it could possibly be treated as an aberrant subgenus within *Simulium* s.l. I have been uncertain as to which is the better course but have decided that, until *gariépense* becomes better known through discovery of its larval stage and biology (when re-assessment of its genus-group status might be made), it is best to place it as a full genus distinct from *Simulium*.

Included taxon. *Afrosimulium gariépense* (de Meillon) **comb. n.**

### **SIMULIUM** Latreille

*Simulium* Latreille, 1802 : 426. Type-species : *Rhagio colombaschensis* Fabricius, 1787, by monotypy.

Diagnosis. ♂♀ : Antenna with 11 segments (very rare exceptions with 10 or 12). Head and eyes normal, latter rarely somewhat reduced in ♀. Last segment of maxillary palp elongate, conspicuously longer than either of the two preceding segments (rare exceptions). Pleural membrane bare or haired. Mesepisternal sulcus narrow and deep, sharply defined and complete. Katepisternum bare or haired, in profile longer than its depth. Costa with spiniform and hair-like macrotrichia. Vein *Rs* simple, *Cu<sub>2</sub>* sinuous. Basal cell absent, or vestigial. Basal section of radius bare or haired. Wing membrane with normal microtrichia. Fore tarsus slender or dilated. Calcipala large (except in Neotropical Andean subgenus *Pternaspatha* Enderlein). Pedisulcus present. ♂ : hypopygium with styles and ventral plate of extremely varied form, ventral plate sometimes toothed; style usually with one apical spinule, spinules multiple in a few forms; parameral hooks very varied, usually many but sometimes only one strong hook each side, sometimes completely vestigial; median sclerite very varied. ♀ : cibarium unarmed or with pointed teeth or blunt granulations between cornuae. Claws with or without basal tooth. Gonapophyses varied, sometimes produced into pointed or tapering curled processes. *Pupa* : Gill of immensely varied form. Abdominal cuticle membranous, without clearly sclerotized terga or sterna and without conspicuous pleural plates or pleurites, abdomen of cast pupal pelt almost entirely pale transparent (except parts of last segment), at most weak pale brownish tergal sclerotization anteriorly; no longitudinally striate areas. Last segment with blunt terminal tubercles, these at most slightly thorn-like. Abdominal onchotaxy with almost constant basic plan (segments 3 and 4 dorsally each with four hooks each side, segments 5-7 ventrally each with two hooks on each side of which those on segment 5 close together and those on 6 and 7 well separated), but aberrant forms of onchotaxy occur (mainly in phoretic forms); dorsum of abdomen with or without backwardly-directed spine-combs on some segments. Cocoon well formed, of discrete shape, with or without neck, sometimes with anterodorsal projection, sometimes reduced to cover only pupal abdomen. *Larva* : Head with cephalic fans, head shape usually not strongly convex. Cephalic apotome broadest near posterior margin (some exceptions in which broadest near middle or well forward). Head pattern positive, negative or unclassifiable. Postgenal cleft of very varied form, sometimes absent, rarely reaching hypostomium. Hypostomium almost always with row of nine apical teeth with only middle tooth and each corner tooth slightly prominent (varied bizarre exceptions occurring, mainly in island or phoretic forms). Mandible varied, nearly always with two serrations on inner margin but these sometimes obliterated or accompanied by one or two supernumerary serrations. Cuticle bare or with setae of various forms and extent of distribution. Ventral papillae present or absent, last abdominal segment almost always without definite accessory ring. Anal sclerite normal X-shaped. Rectal gills simple or compound.

Distribution. Widely distributed in all zoogeographical regions and present almost everywhere on continental land-masses providing suitable watercourses exist for the immature stages. Absent from New Zealand, Hawaii, Samoa and Tonga and coralline islands. Present on following isolated islands : Azores, St. Helena, Seychelles, Réunion, Mauritius, Rodriguez, Ryukyu Islands, Bonin Islands, Mariana Islands, Caroline Islands, New Hebrides, New Caledonia, Fiji, Tahiti, Marquesas Islands. Occurring also throughout East Indian Archipelago and New Guinea, in Iceland, Greenland, Mediterranean islands, Madeira and Canary Islands.

Discussion. *Simulium*, in the broad sense used here and accepted by the majority of simuliid taxonomists, is by far the largest genus of Simuliidae and contains several hundred species—probably amounting to three-quarters or more of the world black-fly fauna. The genus falls into a number of segregates distinguishable by aggregates of characters taken in combination from the adult, pupal and larval stages, and many of the segregates are currently recognized as named subgenera. This course is considered to be the best taxonomic treatment possible, although it has to be admitted that some subgenera are much more distinctive than others and that they cannot all be distinguished by completely satisfactory characters in all stages : some may be virtually inseparable from related subgenera in one sex or one stage, although readily separated by obvious character differences in others.

On a world basis there is as yet no completely worked out and universally applied subgeneric classification for *Simulium* s.l. but at the present time it appears that the world fauna may fall into some 30–35 subgenera, assuming segregates comparable to those already recognized for the Holarctic faunae and recognized in the present paper for the fauna of Ethiopian Africa and Malagasia. Most of the subgenera are endemic to one or confined to two zoogeographical regions, only *Eusimulium* having an almost cosmopolitan range. For Africa and its islands a total of 16 subgenera are here recognized in the *Simulium* fauna : eight of these are confined to the Ethiopian Region (*Anasolen*, *Edwardsellum*, *Freemanellum*, *Lewisellum*, *Meillonellum*, *Metomphalus*, *Phoretomyia* and *Pomeroyellum*) and one to the Malagasy Region (*Xenosimulium*), one occurs only on St. Helena Island (*Dexomyia*), one is common to the Holarctic and Ethiopian Regions (*Byssodon*) and one is cosmopolitan (*Eusimulium*); the remaining four subgenera occur in Palaearctic Africa but are absent from Ethiopian Africa (*Wilhelmia*, *Odagnia*, *Simulium* s. str., *Tetisimulium*) and of these four all except *Simulium* s. str. are confined to the Palaearctic Region (*Simulium* s. str. is present also in the Nearctic and Oriental Regions). Keys for the recognition of the sixteen subgenera occurring in the African area are given below for both sexes and for the pupal and larval stages.

One species occurring in Morocco, *Simulium gracilipes* Edwards, is known only from the female holotype and is subgenerically unplaceable (see Crosskey, 1965 : 667) ; it may belong to the Palaearctic subgenus *Schoenbaueria* Enderlein but this cannot be confirmed on the female alone. However it is possible that future collecting in North Africa may show the presence of this subgenus in the area here covered.

Species of *Simulium* s.l. from other zoogeographical regions sometimes show

characters that never occur in the *Simulium* fauna of the Ethiopian Region. It may therefore be helpful to workers in other regions, who may wish to make quick comparisons of their local fauna with that of Africa, to enumerate some of the characters that are common to all or almost all *Simulium* found in the Ethiopian Region. These characters are found in all *Simulium* species throughout Ethiopian Africa (except where otherwise indicated) :—

- Calcipala well developed.
- Cibarium of ♀ unarmed (except in *S. vorax* and immediate allies).
- Antenna with 11 segments.
- Prothoracic precoxal bridge complete.
- Basal section of radius haired (except *Byssodon* species).
- Style of ♂ hypopygium with one spinule (except in *S. wellmanni*).
- Non-faceted area present on eye adjacent to antennal excavation.
- Frons of ♀ never iridescent.
- Scutum of ♀ never with scale vestiture arranged in small clumps.
- Postgenal bridge of larva complete (even if reduced to very narrow strip medially behind hypostomium).
- Last larval abdominal segment without annular sclerotization.

#### KEYS TO THE SUBGENERA OF *SIMULIUM* IN AFRICA AND ITS ISLANDS

Note : in order not to complicate the keys unnecessarily the first segregation is by geographical area since in practice it will be known whether material originates from Palaearctic Africa or from the Ethiopian and Malagasy Regions; *Eusimulium* is the only subgenus common to both areas and this is run out twice. Likewise with the immature stages of Ethiopian forms it will always be known whether they are phoretic forms associated with crabs or mayfly nymphs, and for convenience they are segregated first in the Ethiopian section of the keys by their phoretic habit : this avoids the difficulty of placing individual phoretic species that are aberrant in certain larval or pupal features. Pupal characters given, especially of the gill or cocoon form, in these keys for Africa will not necessarily hold for extra-limital forms of those subgenera occurring also in other regions. The keys are artificial and juxtaposition of subgenera does not imply close phyletic relationship.

#### MALES

- |   |  |                                      |
|---|--|--------------------------------------|
| 1 | Forms from Ethiopian and Malagasy Regions . . . . .  | 2                                    |
| — | Forms from North Africa and Canary Islands . . . . .   | 14                                   |
| 2 | Basal section of radius bare. Hypopygium as in Text-fig. 95, ventral plate as in Text-figs. 107, 130 . . . . .   | <b>BYSSODON</b> Enderlein (p. 44)    |
| — | Basal section of radius haired. Hypopygium not so . . . . .  | 3                                    |
| 3 | Katepisternum haired. Thoracic ground colour orange-brown to dark reddish brown. Styles long and slender, exceeding length of coxites (Text-figs. 91, 147). Ventral plate as Text-figs. 110-112, 131 . . . . . | <b>FREEMANELLUM</b> sgen. n. (p. 92) |
| — | Katepisternum bare. Thoracic ground colour almost always blackish. Styles at most subequal in length to and usually shorter than coxites. Ventral plate not so . . . . .                                       | 4                                    |
| 4 | Fore tarsi conspicuously enlarged and with dorsal hair-crest (Text-figs. 81, 82), basitarsus 3.5-5 times as long as its greatest breadth (except in <i>berneri</i> ) . . . . .                                 | 5                                    |
| — | Fore tarsi not strongly dilated and without thick hair-crest, basitarsus usually 5.5-8 times as long as its greatest breadth (Text-figs. 78-80, 83) . . . . .  | 6                                    |

- 5 Scutum with sharply defined black and silver-grey pattern (as Text-fig. 77 or with the dark vittae confluent medially). Parameral hooks numerous. Ventral plate strongly arched in profile, toothed, form complex (Text-figs. 118, 136, 137). Style truncate and coxite produced beyond base of style at least slightly (Text-fig. 150). . . . . **EDWARDSELLUM** Enderlein (p. 101)
- Scutum without such pattern. One long strong parameral hook on each side, sometimes rudimentary. Ventral plate lamellate, with small basal arms and not arched in profile or toothed (Text-figs. 106, 128). Style subconical and coxite not produced beyond its base (Text-fig. 146). [Pharate ♂ attached to mayfly nymphs] **PHORETOMYIA** sgen. n. (p. 79)
- 6 Hypopygium with one long strong dagger-shaped or scythe-shaped parameral hook on each side (Text-figs. 88, 89), usually directed outwards and occasionally with one or two supernumeraries at its base. Ventral plate lamellate or subtriangular (Text-figs. 96-101), never toothed and rather straight in profile (Text-figs. 120-127). Scutum without pattern (except in *Dexomyia* from St. Helena) . . . . . 7
- Hypopygium with multiple parameral hooks on each side, at least four or five and usually many (Text-figs. 90, 92). Ventral plate of complex and varied form (Text-figs. 114-117), often toothed and usually strongly angulate in profile (Text-figs. 132-135), sometimes lamellate. Scutum at least with trace of silvery grey shoulder patches, sometimes with bold pattern . . . . . 11
- 7 Scutum patterned as in Text-fig. 310. Pleural membrane sparsely haired. [St. Helena Island only] . . . . . **DEXOMYIA** sgen. n. (p. 49)
- Scutum without pattern. Pleural membrane bare (except in *adersi*) . . . . . 8
- 8 Style abruptly contracted before the apex, usually narrowed on about apical third (Text-fig. 145). Ventral plate longer than broad or subquadrate, with small bent basal arms and median apical approximately U-shaped notch (Text-fig. 105). The parameral hook very conspicuous and with supernumeraries at its base (Text-fig. 89) . . . . . 9
- Style not abruptly narrowed on apical part (Text-figs. 140, 141, 143, 144). Ventral plate transverse or subtriangular in the body with longer basal arms (Text-figs. 96-101). Parameral hook often with one or two supernumeraries arising from its extreme base. . . . . 10
- 9 Small forms, wing-length 1.9-2.5 mm. Basal margin of ventral plate between basal arms slightly bilobate or produced medially . . . . . **MEILLONIELLUM** Rubzov (p. 74)
- Large forms, wing-length 2.6-3.6 (usually about 3.0) mm. Basal margin of ventral plate between basal arms more or less smoothly rounded. [Pharate ♂ attached to crabs] . . . . . **LEWISELLUM** sgen. n. (p. 76)
- 10 Ventral plate strongly transverse, with median keel and shoulders well developed (Text-figs. 88, 101) . . . . . **EUSIMULIUM** Roubaud (p. 56)
- Ventral plate less strongly transverse, anterolateral shoulders sloped or plate subtriangular (Text-figs. 96-98), if plate transverse then without strong median keel (Text-fig. 99) . . . . . **POMEROYELLUM** Rubzov (p. 66)
- 11 Scutum with silver-grey pruinose shoulder marks or with a bold black and pale grey pattern (Text-fig. 76 or similar to Text-fig. 75). Ventral plate of diverse form (Text-figs. 114-117, 133-135), most often subtriangular and toothed apically (Text-fig. 92). Pleural membrane bare (except in *letabum* and *natalense*) **METOMPHALUS** Enderlein (p. 96)
- Scutum without silvery grey shoulder marks or black and grey pattern. Ventral plate differently formed, never toothed. Pleural membrane bare or haired . . . . . 12
- 12 Ventral plate very broad rectangular (Text-fig. 103), usually with haired bent mid-apical lip. Pleural membrane bare **loutetense**-group **EUSIMULIUM** (p. 63)
- Ventral plate narrower, less flat and rectangular. Pleural membrane usually haired . . . . . 13

- 13 Ventral plate with well developed shoulders and parallel basal arms, haired across most of width of apical margin (Text-fig. 104), plate only slightly curved in profile (Text-fig. 129). Style not abruptly truncate (Text-fig. 148). [Malagasy Region only] . . . . . **XENOSIMULIUM** sgen. n. (p. 86)
- Ventral plate with more sloping shoulders, or subtriangular (Text-figs. 108, 109) in profile body of plate strongly bent or angulate in relation to basal arms (Text-fig. 132). Style rather truncate apically (Text-fig. 149). [Ethiopian Region only, including southern Arabia] . . . . . **ANASOLEN** Enderlein (p. 88)
- 14 Basal section of radius bare. Styles long and heavy, conspicuous in situ, subparallel-sided and very much longer than coxites (Text-figs. 94, 155) . . . . . 15
- Basal section of radius haired. Styles shorter than or at most subequal in length to coxites . . . . . 17
- 15 Pleural membrane bare . . . . . **SIMULIUM** Latreille s. str. (p. 110)
- Pleural membrane haired . . . . . 16
- 16 Fore tarsus slender, basitarsus 7–8 times as long as its greatest breadth (Text-fig. 85). Ventral plate Y-shaped, in profile without beak-like projection (Text-fig. 138) . . . . . **TETISIMULIUM** Rubzov (p. 104)
- Fore tarsus flattened and dilated, basitarsus 4–5.5 times as long as its greatest breadth (Text-figs. 86). Ventral plate as Text-fig. 119, in profile with haired beak-like projection (Text-fig. 139) . . . . . **ODAGMIA** Enderlein (p. 107)
- 17 Pleural membrane bare. Ventral plate broad lamellate (Text-figs. 100, 101) with subparallel basal arms (except in *aureum*-group with small triangular plate and divergent arms, Text-fig. 102). Style not folding down against coxite. Only one main parameral hook on each side. . . . . **EUSIMULIUM** Roubaud (p. 56)
- Pleural membrane haired. Ventral plate subtriangular with large divergent basal arms (Text-figs. 93, 113). Style very small and capable of folding down against large coxite (Text-fig. 151). Parameral hooks numerous (Text-fig. 93) . . . . . **WILHELMIA** Enderlein (p. 94)

## FEMALES

- 1 Forms from Ethiopian and Malagasy Regions . . . . . 2
- Forms from North Africa and Canary Islands . . . . . 13
- 2 Basal section of radius bare . . . . . **BYSSODON** Enderlein (p. 44)
- Basal section of radius haired . . . . . 3
- 3 Head abnormal, eyes small and in profile only a little wider than postocular part of head (Text-fig. 69), in dorsal view frons almost as wide as one eye (Text-fig. 71). [St. Helena Island only] . . . . . **DEXOMYIA** sgen. n. (p. 49)
- Head normal, eyes occupying most of sides of head and frons conspicuously narrower than one eye in dorsal view (Text-figs. 66, 70). [Not from St. Helena, except one species of *Eusimulium*] . . . . . 4
- 4 Katepisternum haired. Ground colour of thorax reddish to dark red-brown. Gonapophyses fleshy and protruberant downwards, paraprocts also slightly or strongly produced ventrally (Text-fig. 163) . . . . . **FREEMANELLUM** sgen. n. (p. 92)
- Katepisternum bare. Ground colour of thorax almost always blackish. Gonapophyses and paraprocts not so . . . . . 5
- 5 Fore tarsi conspicuously dilated and with thick dorsal hair-crest (Text-figs. 81, 82), basitarsus 3.5–5 times as long as its greatest breadth . . . . . 6
- Fore tarsi not enlarged and flattened and without conspicuous hair-crest (Text-figs. 78–80), basitarsus usually 5.5–8 times as long as its greatest breadth . . . . . 7
- 6 Hind basitarsus creamy white on most of its length and contrasting conspicuously with black remainder of tarsus. Gonapophyses forming slender curled acuminate processes (Text-fig. 159). Spermatheca with long internal hairs. Scutum with

- bluish grey bloom seen from in front, finely and inconspicuously pale scaled  
**EDWARDSSELLUM** Enderlein (p. 101)
- Hind tarsus entirely black without contrasting pale base. Gonapophyses bluntly rounded lobes, not at all produced. Spermatheca without internal hairs. Scutum thickly brilliant pale yellow to deep golden scaled, sometimes with bronze-coppery scales medially, no trace of such bloom  
**PHORETOMYIA** sgen. n. (p. 79)
- 7 Gonapophyses forming pointed subtriangular or slender attenuated processes (Text-figs. 158-161). Claws simple or with minute basal tooth (Text-fig. 83). Pleural membrane often haired . . . . . 8
- Gonapophyses forming short bluntly rounded or truncate lobes (Text-figs. 156, 157). Claws usually with very large basal tooth (Text-figs. 78, 79). Pleural membrane bare (except in *adersi*) . . . . . 10
- 8 Gonapophyses forming rather large clasper-like processes directed towards each other and strongly haired apically (Text-fig. 161). Paraprocts slightly attenuated ventrally. Seventh abdominal segment with distinctly formed brownish sclerotized sternite. [Malagasy Region only] . . . . . **XENOSIMULIUM** sgen. n. (p. 86)
- Gonapophyses not of this form. Paraprocts not produced downwards. Seventh abdominal segment with distinct sternite, pale and membranous ventrally [not known from Malagasy Region] . . . . . 9
- 9 Gonapophyses forming long narrow acuminate processes, usually curled (Text-figs. 159, 160, 162). Scutum normally with a lyrate dark pattern (of type shown in Text-fig. 72), sometimes only visible from in front in certain lights. Spermatheca with internal hairs. Claws simple . . . . . **METOMPHALUS** Enderlein (p. 96)
- Gonapophyses short subtriangular with tips slightly pointed and directed slightly inwards (Text-fig. 158), inner margins concave. Scutum without definite pattern. Spermatheca without internal hairs. Claws with very small basal tooth or sometimes almost simple . . . . . **ANASOLEN** Enderlein (p. 88)
- 10 Claws with large basal tooth (Text-figs. 78, 79) (except in *speculiventre* from Seychelles). Small forms, wing-length usually 1.8-2.8 mm, hind tibiae usually with sub-basal dark band and legs extensively pale, body scaling usually silvery yellow or silvery. [Pharate females not attached to other arthropods] . . . . . 11
- Claws with very small or minute basal tooth, sometimes virtually simple (Text-fig. 80). Larger forms, wing-length 2.7-3.6 mm, legs usually entirely black and hind tibiae therefore without sub-basal dark band, body scaling brilliant pale yellow to deep golden. [Pharate females attached to crabs or mayfly nymphs] . . . . . 12
- 11 Abdominal tergites 6-8 bare except for sparse fine inconspicuous hairing and semi-shining black (except fully pale scaled in *merops* and *evillense*)  
**POMEROYELLUM** Rubzov (p. 66)
- Abdomen evenly and thickly covered with pale scales, not almost bare and shining on terminal segments  
**EUSIMULIUM** Roubaud (p. 55), **MEILLONIELLUM** Rubzov (p. 74)
- 12 First two abdominal segments thickly covered with brilliant pale yellow to deep golden scales and strongly contrasting with remainder of abdomen which is black with coppery brown scaling, and at most has only scattered yellow scaling laterally. [Pharate ♀ attached to mayfly nymphs] **PHORETOMYIA** sgen. n. (part) (p. 79)
- Abdomen rather thickly and evenly covered with pale yellow to golden scales, sometimes with dark coppery scales in addition, not therefore strongly contrasting in appearance between basal segments and remainder of abdomen\*. [Pharate ♀ attached to crabs]. . . . . **LEWISSELLUM** sgen. n. (p. 76)
- 13 Basal section of radius haired. Cibarium unarmed . . . . . 14
- Basal section of radius bare. Cibarium armed with minute denticles or granulations between the cornuae . . . . . 15
- 14 Claws simple, very enlarged (Text-fig. 84). Pleural membrane haired. Gona-

\* See Appendix

- pophyses produced into slender curled processes (Text-fig. 159). Scutum pale greyish with dark lyrate pattern (Text-fig. 72) **WILHELMIA** Enderlein (p. 94)
- Claws with very large basal tooth (Text-fig. 79). Pleural membrane bare. Gonapophyses simple truncate lobes (Text-fig. 156). Scutum without pattern **EUSIMULIUM** Roubaud (p. 56)
- 15 Pleural membrane bare. Claws simple **SIMULIUM** Latreille s. str. (p. 110)
- Pleural membrane haired. Claws with very small basal tooth (Text-figs. 85, 86) . . . 16
- 16 Scutum pale greyish with three broad longitudinal brown or blackish vittae (Text-fig. 73). Fore tarsus slender, basitarsus 7–8 times as long as its greatest breadth (Text-fig. 85). Abdomen with three lines of dark spots on pale greyish ground **TETISIMULIUM** Rubzov (p. 104)
- Scutum blackish with silvery greyish pattern anteriorly (Text-fig. 74). Fore tarsus dilated, basitarsus 4–5 times as long as its greatest breadth (Text-fig. 86). Abdomen dull blackish basally and shining black on tergites 6–8, not maculate **ODAGMIA** Enderlein (p. 107)

## PUPAE

- 1 Forms from Ethiopian or Malagasy Regions . . . . . 2
- Forms from North Africa and Canary Islands . . . . . 13
- 2 Pupae attached to mayfly nymphs\*. Cocoon often covering only the pupal abdomen. Abdominal onchotaxy sometimes aberrant (Text-figs. 170, 173) **PHORETOMYIA** sgen. n. (p. 79)
- Pupae not attached to mayfly nymphs. Cocoon not reduced (except in *gyas* from Madagascar). Abdominal onchotaxy normal (except in *Dexomyia* from St. Helena) . . . . . 3
- 3 Pupae attached to river-crabs. Gill with eight long slender filaments, usually longer than pupal body, arranged 3+3+2 (Text-fig. 195) **LEWISSELLUM** sgen. n. (p. 76)
- Pupae not attached to crabs. If gill with eight filaments not of this form (except similar in some *Meillonellum*, Text-fig. 193) . . . . . 4
- 4 Abdominal segments 5–7 ventrally with aberrant onchotaxy (Text-fig. 323), each with irregular transverse row of many hooks (numbering variable from 6–24 on each segment). Gill with four filaments as Text-fig. 322. [St. Helena Island only] . . . . . **DEXOMYIA** sgen. n. (p. 49)
- Abdominal segments 5–7 ventrally with normal onchotaxy (Text-fig. 171), each with one pair of hooks on each side, those of segment 5 closer together than those on 6 and 7 (*bovis*-group without hooks or with only a single pair on segment 5). Gill not as Text-fig. 322 . . . . . 5
- 5 Gill trifold or bifid with flattened lanceolate, subcylindrical or subspherical branches directed forwards (Text-figs. 221, 222). Terminal abdominal tubercles pointed thorn-like, directed backwards . . . . . **BYSSODON** Enderlein (p. 44)
- Gill not with this form. Terminal abdominal tubercles usually very blunt . . . . . 6
- 6 Abdominal segments 6–8 bare dorsally. Cocoon shoe-shaped, with well developed neck (except *albivirgulatum* with incomplete neck and *gyas* with reduced cocoon) . . . . . 7
- Some or all of abdominal segments 6–8 (sometimes also 9) with well developed backwardly directed spine-combs (Text-fig. 168). Cocoon simple and slipper-shaped (Text-fig. 164), rarely with weak neck . . . . . 11
- 7 Gill with four filaments (Text-figs. 205, 206) . . . . . **FREEMANELLUM** sgen. n. (p. 92)
- Gill with more than four filaments or branches . . . . . 8
- 8 Gill filaments with sharp pointed blackened tips (Text-figs. 203, 204), of one type and numbering 8–19 . . . . . **ANASOLEN** Enderlein (p. 88)
- Gill filaments without sharp darkened tips . . . . . 9

\* or to river prawns, see Appendix

- 9 Gill formed of six or nine large thin-walled tubular filaments arising between a pair of large inflated basal arms (Text-figs. 209, 210), all branches pale and of essentially the same kind . . . . . **EDWARDSSELLUM** Enderlein (p. 101)  
 - Gill with filaments not of this type (except in *cavum* and *natalense*) . . . . . 10
- 10 Gill with one type of slender filament and without basal arms, filaments numbering 6-19 (Text-figs. 200-202). [Malagasy Region only] **XENOSIMULIUM** sgen. n. (p. 86)  
 - Gill with stout primary filaments and thinner secondary filaments or with enlarged tubular branches, often with basal arms (Text-figs. 211-216), if filaments all slender except at the base (Text-fig. 214) then numbering at least 24. [Ethiopian Region only] . . . . . **METOMPHALUS** Enderlein (p. 96)
- 11 Gill with four filaments (Text-figs. 174, 175, 177-180) (except in *loutetense* with six filaments as Text-fig. 176 and cocoon with neck) **EUSIMULIUM** Roubaud (p. 56)  
 - Gill not with four filaments (only with six filaments in *sexiens* but then cocoon simple) . . . . . 12
- 12 Gill filamentous, with 6, 8 or 11 filaments (Text-figs. 193, 194) . . . . . **MEILLONIELLUM** Rubzov (p. 74)  
 - Gill of very varied form (Text-figs. 181-192, 196) but never with 6 or 11 filaments and if with 8 filaments these not arranged as in Text-fig. 193 . . . . . **POMEROYELLUM** Rubzov (p. 66)
- 13 Gill of filamentous type with 4, 6 or 8 filaments. At least one of the abdominal segments 6-9 with dorsal spine-combs . . . . . 14  
 - Gill with a pair of large inflated thin-walled basal arms bearing thin-walled variously modified tubes between them (often with form similar to Text-fig. 207). Abdominal segments 6-9 bare dorsally, all without trace of spine-combs . . . . . **WILHELMIA** Enderlein (p. 94)
- 14 Gill with four filaments . . . . . **EUSIMULIUM** Roubaud (p. 56)  
 - Gill with more than four filaments . . . . . 15
- 15 Gill with eight filaments arising in regular pairs (Text-fig. 220). Cocoon simple, slipper-shaped without neck . . . . . **ODAGMIA** Enderlein (p. 107)  
 - Gill with six filaments. Cocoon with loosely woven neck showing large open fenestrations (Text-fig. 218) . . . . . 16
- 16 Gill as in Text-fig. 217. Dorsum of eighth abdominal segment with spine-comb . . . . . **TETISIMULIUM** Rubzov (p. 104)  
 - Gill as in Text-fig. 219. Dorsum of ninth abdominal segment with spine-comb . . . . . **SIMULIUM** Latreille s. str. (p. 110)

## LARVAE

[Note: the key applies only to older and mature larvae and cannot be used for the early instars, which for almost all forms are either unknown or have not been studied in detail]

- 1 Forms from Ethiopian and Malagasy Regions . . . . . 2  
 - Forms from North Africa and Canary Islands . . . . . 14
- 2 Larvae attached to crabs. Hypostomium with rather even row of 13 apical teeth (Text-fig. 268). Mandible tapering-elongate and very little arched on outer edge (Text-fig. 292). Body form as Text-fig. 284. Head elongate and cephalic apotome rounded posteriorly (Text-fig. 283) . . . . . **LEWISELLUM** sgen. n. (p. 76)  
 - Larvae not attached to crabs. Hypostomium, mandible, body form and shape of cephalic apotome not so . . . . . 3
- 3 Larvae attached to mayfly nymphs\*. Posterior cirlet in a subventral position (Text-fig. 285). Cephalic fans when open sometimes forming short flat brushes (Text-fig. 286). Hypostomium sometimes of form shown in Text-fig. 267 . . . . . **PHORETOMYIA** sgen. n. (p. 79)  
 - Larvae not attached to mayfly nymphs. Posterior cirlet in the normal terminal position. Cephalic fans when open always forming normally shaped curved brushes. Hypostomium never of this form . . . . . 4

\* or to river prawns, see Appendix.

- 4 Cephalic fan with two types of ray, a few very stiff strongly sclerotized blackened rays clearly differentiated from fine pale rays on either side (Text-fig. 325). Head with strongly convex sides and cephalic apotome broadest near the middle (Text-fig. 325). Hypostomium with group of deeply sunken median teeth flanked by two very prominent groups (Text-fig. 326). Dorsum of cuticle coarsely shagreened. [St. Helena Island only] . . . . . **DEXOMYIA** sgen. n. (p. 49)
- Cephalic fans normal, rays not clearly differentiated into these two types. Head normal, sides not strongly convex and cephalic apotome widest posteriorly. Hypostomium not of this shape. Surface of cuticle more or less smooth . . . . . 5
- 5 First five abdominal segments with paired dorsolateral subconical tubercles (Text-fig. 230). Most of thoracic and abdominal cuticle, including the proleg, extensively covered with elongate scale-like setae (Text-figs. 230, 231); setae particularly aggregated on abdominal tubercles and making these conspicuous even when smaller than normal. Postgenal cleft exceptionally large and subcircular (Text-fig. 261), occupying most of venter of head capsule  
**EDWARDSSELLUM** Enderlein (p. 101)
- Abdominal segments without paired dorsolateral swellings, at most slightly produced but then without covering of setae. Body cuticle usually without such vestiture, if (*albivirgulatum*-group) with conspicuous simple scales these not extending on to proleg. Postgenal cleft usually not of this form . . . . . 6
- 6 Cuticle of both thoracic and abdominal dorsum with large flat scales, very easily visible. Postgenal cleft elongate subelliptical (Text-fig. 259). Apex of hypostomium as in Text-fig. 281, two teeth at each end of the normal row of nine unusually strong and produced forwards. Outline of body shape as Text-fig. 287  
**albivirgulatum**-group (**METOMPHALUS**)
- Cuticle bare or with different vestiture, if abundant setae present on cuticle of both thorax and abdomen then minute and hair-like or fan shaped, if large erect scale-like setae present these confined to posterodorsal part of abdomen. Postgenal cleft not of this shape. Hypostomium normal. Body shape as in Text-figs. 224, 226, 228 . . . . . 7
- 7 Dorsum of thorax and abdomen with minute inconspicuous erect fan-shaped setae and abdomen without ventral papillae. Mandible with one serration only on inner margin, or at most only a trace of second. Head capsule almost totally unpigmented . . . . . **BYSSODON** Enderlein (p. 44)
- Cuticle either without deeply divided fan-shaped setae, or if these present then lying mainly recumbent and abdomen with ventral papillae. Mandible with two or more serrations, inner margin rarely irregularly jagged. Head capsule normally with distinct pigmentation (except sometimes creamy white without obvious marking in *bovis*-group) . . . . . 8
- 8 Ventral papillae present, subconical (Text-fig. 224), sometimes small and rounded. Rows of hypostomial setae lying subparallel to lateral margins of hypostomium (Text-figs. 269-273, 303), median and corner teeth of hypostomium usually strongly prominent (Text-figs. 271-273). Mandible with middle comb-tooth smaller than first or third (Text-fig. 291). Body form usually as in Text-fig. 224. Head pattern usually negative (Text-figs. 232-234). Posterior cirlet with fewer hooks (from 60-115 rows of 8-16 hooks). Antennae usually long and slender (Text-fig. 289), longer than stem of cephalic fan . . . . . 9
- Ventral papillae absent (Text-figs. 226, 228). Rows of hypostomial setae diverging posteriorly from lateral margins of hypostomium (Text-figs. 275-279, 304), median and corner teeth of hypostomium not strongly prominent (Text-figs. 276-280). Mandible with large comb-teeth forming a regularly graded or subequal series (Text-figs. 300-302). Body form as in Text-figs. 226 or 228. Head pattern always positive (Text-figs. 237-240). Posterior cirlet with conspicuously

- numerous hooks (from 110–300 rows of 18–49 hooks). Antennae short (Text-fig. 288), usually not longer than stem of cephalic fan . . . . . 11
- 9 Head-spots positive (Text-figs. 235, 236). Cuticle bare or at most with minute colourless and very inconspicuous simple hairs. Postgenal cleft very small, much shorter than postgenal bridge (Text-figs. 241–244) (except in *loutetense*-group, Text-fig. 245) . . . . . **EUSIMULIUM** Roubaud (p. 56)
- Head pattern negative, on cephalic apotome pale spots separated or surrounded by dark pigmentation that often forms an H-shaped mark (Text-figs. 232–234). Cuticle at least of the abdomen with simple or variously modified setae (except bare in *bequaerti*-group). Postgenal cleft normally longer than or at least subequal in length to postgenal bridge (Text-figs. 246–250) . . . . . 10
- 10 Abdominal cuticle posterodorsally with sparse minute simple or at most slightly fusiform setae. Postgenal cleft large and rounded-subcordate (Text-fig. 250). Ventral papillae sometimes rounded and small, rather inconspicuous . . . . . **MEILLONIELLUM** Rubzov (p. 74)
- Abdominal cuticle posterodorsally with large erect scales or small more recumbent divided setae (of shapes shown in Text-fig. 225), bare in *bequaerti*-group. Postgenal cleft variously shaped but not of this form. Ventral papillae subconical, well developed . . . . . **POMEROYELLUM** Rubzov (p. 66)
- 11 Abdominal cuticle bare. Primary brush of the mandible exceptionally prominent beyond end of mandible, often strongly arched (Text-figs. 295, 296). Main apical tooth of mandible unusually reduced in size relative to other teeth (Text-figs. 301, 302), not noticeably stronger than or even smaller than comb-teeth. Sides of hypostomium (outside the rows of setae) broadly expanded and hypostomial teeth very reduced (Text-figs. 276, 277) . . . . . 12
- Abdominal cuticle, at least posterodorsally, with small scales (Text-figs. 228, 229) or with minute scattered simple setae (Text-figs. 226, 227). Primary brush of mandible normal, not projecting far beyond apex (Text-fig. 294). Main apical tooth of mandible of normal large size, conspicuously larger than comb-teeth and other apical teeth (Text-fig. 300). Sides of hypostomium less widely dilated and hypostomial teeth less reduced (Text-figs. 275, 278–280) . . . . . 13
- 12 Rectal gills with numerous finger-like secondary lobules. Antenna four-segmented, without secondary annulations. Postgenal cleft large and mitre-shaped (Text-fig. 254), much longer than postgenal bridge. [Ethiopian Region only] . . . . . **FREEMANELLUM** sgen. n. (p. 92)
- Rectal gills simple trilobate, without secondary lobules. Antenna with 6–8 apparent segments because of secondary annulation (Text-fig. 290). Postgenal cleft smaller and more pentagonal (Text-fig. 255), not longer than postgenal bridge. [Malagasy Region only] . . . . . **XENOSIMULIUM** sgen. n. (p. 86)
- 13 Postgenal cleft very small, much shorter than postgenal bridge and forming a subquadrate or slightly pentagonal notch (Text-fig. 253). Hypostomial setae numerous, 8–24 (usually 12–18) in each row. Abdomen only with simple setae (these so small and sparse that superficially abdomen may appear bare). Rectal gills always with many secondary lobules. . . . . **ANASOLEN** Enderlein (p. 88)
- Postgenal cleft large and much longer than postgenal bridge, broadly sagittate, subcordate or subcircular (Text-figs. 256–258, 260). Hypostomial setae usually fewer, 3–10 in each row. Abdomen with simple setae or with small flat scale-like setae (Text-fig. 229). Rectal gills simple or compound . . . . . **METOMPHALUS** Enderlein (p. 96)
- 14 Abdomen with subconical ventral papillae. Postgenal cleft much shorter than postgenal bridge, usually forming only a small subquadrate notch in posteroventral head margin (Text-fig. 241). Middle comb-tooth of mandible shorter than either first or third. Pupal gill histoblast with four filaments . . . . . **EUSIMULIUM** Roubaud (p. 56)

- Abdomen without ventral papillae or with small rounded ventrolateral swellings. Postgenal cleft usually large and longer than postgenal bridge. The three comb-teeth of mandible regularly decreasing in size or second and third subequal to each other. Pupal gill histoblast not with four filaments . . . . . 15
- 15 Postgenal cleft large pentagonal (Text-fig. 263), broadly sagittate or subcordate, much longer than postgenal bridge. Ventral papillae absent . . . . . 16
- Postgenal cleft small or medium-sized, rounded and shorter than postgenal bridge (Text-fig. 264). Last abdominal segment with distinct fold-like swellings in lateroventral position . . . . . **ODAGMIA** Enderlein (p. 107)
- 16 Cuticle entirely bare. Rectal gills with or without secondary lobules . . . . . 17
- Cuticle of abdomen posterodorsally with scattered minute deeply divided trifid setae. Rectal gills without secondary lobules . . . . . **WILHELMIA** Enderlein (p. 94)
- 17 Rectal gills with secondary lobules . . . . . **SIMULIUM** Latreille s. str. (p. 110)
- Rectal gill lobes simple, without secondary lobules . . . . . **TETISIMULIUM** Rubzov (p. 104)

#### SYSTEMATIC TREATMENT OF THE SUBGENERA

##### Subgenus **BYSSODON** Enderlein

*Byssodon* Enderlein, 1925 : 209. Type-species : *Simulium forbesi* Malloch, 1914 [= *Simulium meridionale* Riley, 1887], by original designation.

*Psilocnetha* Enderlein, 1935 : 359. Type-species : *Psilocnetha scapulata* Enderlein, 1935 [= *Simulium griseicolle* Becker, 1903], by original designation. **Syn. n.**

*Titanopteryx* Enderlein, 1935 : 360. Type-species : *Atractocera maculata* Meigen, 1804, by original designation.

*Echinosimulium* Baranov, 1938 : 317, 322. Type-species : *Echinosimulium echinatum* Baranov, 1938 [= *Atractocera maculata* Meigen, 1804], by original designation.

*Gibbinsiellum* Rubzov, 1962 : 1494. Type-species : *Simulium griseicolle* Becker, 1903, by original designation. **Syn. n.**

Diagnosis. ♂♀ : Basal section of radius bare. Pleural membrane bare. Katepisternum bare. Fore tarsus slender, fore basitarsus about 6-7 times as long as its greatest breadth. ♀ : cibarium unarmed. Tarsal claws with very large basal tooth (Text-fig. 87). Scutum with inconspicuous lyrate pattern (of same form as *Wilhelmia*, Text-fig. 72), in one species with pair of rounded anterior black-brown spots. Abdomen thickly covered with silvery hair or scales, sometimes mainly laterally. Seventh sternite undeveloped or very weak. Gonapophyses simple bluntly truncate lobes. Genital fork with well formed thumb-like anterior process pre-apically on each arm. Paraprocts normal although acuminate ventrally. Spermatheca without polygonal pattern or internal hairs. ♂ : scutum largely black but with greyish pollinose margins, seen from in front showing trace of three fine dark lines similar to those of ♀. Genitalia with large truncate styles subequal in length to or a little shorter than coxites (Text-fig. 154), style with one apical spinule ; coxite not produced beyond base of style ; ventral plate broad lamellate with short parallel basal arms, haired and without teeth ; median sclerite strap-like or large dilated and bifurcate ; parameres small and narrow or irregular, parameral hooks large and numerous (varied in size). *Pupa* : Gill of varied form, arborescent (with 22-26 filaments) or bifid or trifid with the branches flattened and lanceolate or subcylindrical or subspherical ; gill much shorter than pupal body. Abdominal onchotaxy normal, sometimes pair of supernumerary hooklets ventrally on segment 4 and with or without minute spinous hooklets dorsally on segment 2 ; dorsum without spine-combs or with a few backwardly-directed spines (not forming a close-set comb) on segment 8 and sometimes also segment 7 ; terminal tubercles rather pointed thorn-like, directed backwards. Cocoon simple or with narrow neck, not fenestrate and without median dorsal projection. *Larva* : Head and cephalic fans normal (but unusually

pale and weakly sclerotized). Hypostomium with usual nine apical teeth, median and corner teeth strongly prominent (Text-fig. 274); only 2-4 setae in each hypostomial row, rows lying parallel to lateral margins of hypostomium, serrations prominent. Head pale, largely unpigmented, sometimes a little pigmentation on cephalic apotome but pattern neither clearly positive or negative (sometimes areas where spots normally present rather paler than surroundings). Postgenal cleft very large and reaching or almost reaching hypostomium, postgenal bridge therefore incomplete or forming only narrow strip between apex of cleft and base of hypostomium, if bridge incomplete then cleft widely reaching hypostomium. Mandible normal, middle comb-tooth usually weaker than first or third, sometimes subequal to third; inner mandibular margin rather convex, one serration with or without trace of a small blunt second serration. Antenna of medium length, unpigmented, with four segments (except occasionally first suture apparently obliterated). Thoracic and abdominal cuticle dorsally covered with minute erect fan-shaped or scale-like setae. Abdomen with dorsolateral prominences, slightly subconical, on first five or six segments, or if not at least with the mid ventral part of each of the first few segments unusually prominent (segmentation of the narrow anterior part of abdomen therefore always well marked). Ventral papillae small and subconical or virtually absent. Accessory sclerites absent (or rarely slight trace). Rectal scales present. Rectal gills with numerous secondary lobules. Posterior circlet with about 60-65 rows of 9-15 hooks.

Bionomy. [Oviposition sites apparently unrecorded, eggs probably laid broadcast on water.] Larval and pupal stages non-phoretic; attached to submerged sticks, grasses, sedge, corn-stalks, fish-traps and other substrates in smooth or slightly broken but moderately swift waters of large or very large rivers. Female ornithophilic or sometimes mammalophilic (including anthropophilic when occurring in large outbreaks).

Distribution. Scattered distribution throughout the mainland of the North American, Eurasian and African continents. African distribution as in Map 11.

Discussion. *Byssodon* is the only subgenus of *Simulium* s.l. in the Ethiopian Region that has the basal section of the radius bare, and on account of this and several other of its characters it is markedly isolated from all the endemic Ethiopian subgenera: it is also the only subgenus (except for the cosmopolitan *Eusimulium*) which is common to the Palaearctic and Ethiopian Regions. Rubzov (1959-1964), in his monograph of Palaearctic Simuliidae, used the name *Titanopteryx* Enderlein for the segregate, but Stone (1963) showed that the name *Byssodon* Enderlein applies to the same concept and therefore that *Titanopteryx* falls as a synonym. This is unquestionably correct, and in fact the type-species of *Byssodon* (*Simulium meridionale* Riley) and of *Titanopteryx* (*Simulium maculatum* (Meigen))—although the one is from North America and the other from western Europe—have such identical characters that they might even be synonymous. Baranov's genus-group name *Echinosimulium* is also, as Stone (1963) noted, a synonym of *Byssodon* since (through the synonymy of its type-species with *maculatum* Meigen) it is an isogenotypic synonym of *Titanopteryx*.

The synonymy of *Psilocnetha* with *Byssodon*, which is here newly established, is not so clear-cut, but as the result of studies on the segregates of *Simulium* s.l. on a world basis it has become apparent that the distinctions between the Ethiopian *Psilocnetha* and Holarctic *Byssodon* are inadequate to justify the separation of the two segregates as subgenera (although they are recognized here as separate species

groups). The adults are inseparable, and agree for instance in having the base of the radius bare, the fore tarsi slender, a very large basal tooth to the female claw, bare pleural membrane, unarmed cibarium, similarly marked scutum, and exactly similar form of male hypopygium (Text-fig. 95); especially characteristic is the presence in the females of both *Psilocnetha* and *Byssodon* of an elongate thumb-like or finger-like anterior process on each arm of the genital fork (a much more slender and drawn-out process than occurs in other segregates), a striking feature that supports the present conclusion that *Psilocnetha* must be treated in synonymy with *Byssodon*. There are differences in the immature stages (indicated below in the diagnoses of the species-groups), but the overall resemblance in larval facies also supports the proposed synonymy: in both the Holarctic and the Ethiopian forms involved the larval head is usually pale and weakly sclerotized, the postgenal cleft is enormous and occupies most of the venter of the cranium, the mandibular serrations are usually reduced to one, the rectal gills are much subdivided, and the thoracic and abdominal cuticle is covered with small erect setae on the dorsal side; they even conform in detail of the small number of rows of hooks in the posterior circlet.

The new synonymy of *Psilocnetha* and *Byssodon* is supported by the unusual ecological requirements of both the former in Africa and the latter in North America and Eurasia; the immature stages are found almost exclusively in the very largest rivers and their more major affluents, where they often form the only component of the *Simulium* s.l. fauna present. In North America *Byssodon* breeds mainly in the rivers of the south-western half of the United States, including especially the Mississippi River (type-locality of the type-species, *meridionale* Riley) and in Eurasia in the large European, Russian and Siberian rivers (such as the Po, Danube, Dnieper, Volga, Yenisei, Lena and Kolyma); likewise, the *griseicolle*-group of *Byssodon* occurs in the great rivers of Africa, including the Nile, Congo, Benue, Niger and Volta. A biological adaptation clearly exists in all these forms for a preimaginal existence in moderately swift but most often unbroken waters that allows species of the subgenus *Byssodon* to thrive in long stretches of the very largest rivers, where other segregates of *Simulium* s.l. are usually absent, although occasional coexistence with other segregates sometimes occurs: for instance, *S. (Byssodon) maculatum* in Europe may occur in admixture with *S. (Wilhelmia) equinum* L., and *S. (Simulium) colombaschense* (Fabricius), and in Africa *S. (Byssodon) griseicolle* sometimes coexists with *S. (Meilloniellum) adersi* Pomeroy or *S. (Edwardsellum) damnosum* Theobald.

The ecological adaptation of *Byssodon* to very large rivers may provide a clue to the otherwise rather anomalous position of this segregate in the fauna of *Simulium* south of the Sahara. All the *Simulium* s.l. of the Ethiopian Region other than *Byssodon* (and excluding the almost cosmopolitan subgenus *Eusimulium*) belong to endemic subgeneric segregates, all with haired base to the radius, that appear to have arisen after long isolation south of the desert and to have diverged from their Arctogaeon counterparts to such an extent that there is no longer a high correspondence of characters. In *Byssodon*, however, the only subgenus in Africa south of

the Sahara in which the radius is bare basally, isolation has certainly been less complete and the valley of the Nile provides a linking route of almost continuous distribution from Europe via the Middle East (where a species of *Byssodon* occurs at least in the Tigris and Jordan valleys) to Egypt and the Sudanese Nile and hence to Ethiopian Africa : a group of Simuliidae able to utilize the fluvial habitat provided by the Nile itself would be able to disperse between the Palaearctic and Ethiopian Regions at periods such as recent geological times when conditions of extreme drought over wide areas imposed severe barriers against the dispersal of most forms. The existence of the Nile is tentatively suggested as the explanation for the occurrence of *Byssodon* segregate in both Africa and Eurasia, a group otherwise so disjunct from the other elements in the Ethiopian fauna (excepting perhaps *Afro-simulium* q.v.).

The Middle Eastern species of *Byssodon* cited above is *Simulium* (*Byssodon*) *buxtoni* Austen from Palestine and Iraq. This very small species in which the scutum of the female has a pair of anterior rounded black-brown spots (figured by Crosskey, 1967b : 11) is unfortunately still known only from the adult female, but the genital fork and all other characters confirm its position in *Byssodon*. In an earlier paper (Crosskey, 1967b) I assigned the species, under the name *irakae* Smart, to *Psilocnetha* but since this genus-group name is here sunk to *Byssodon* the Middle Eastern species is re-assigned accordingly. Dr. Alan Stone (personal communication) has very kindly pointed out to me that Smart (1944) did not need to provide his replacement name *irakae* for the preoccupied *Simulium bipunctatum* Austen because *S. bipunctatum* var. *buxtoni* Austeni was held to be conspecific with typical *bipunctatum* and the species-group name *buxtoni* was therefore nomenclaturally available for the species concerned : the species referred to as *irakae* Smart in my previous paper (Crosskey, 1967b) should be known under the rules of nomenclature as *buxtoni* Austen, and *irakae* Smart falls as a junior synonym of this name.

*Simulium transiens* Rubzov from Siberia and Canada has been assigned to *Byssodon* by Rubzov (1940, 1959-1964 : 427) and by Stone (1965), but Rubzov (1959-1964 : 623) erected the genus *Parabyssodon* Rubzov, 1964 as a monotypic genus for this species. I have examined adult, pupal and larval material of *transiens* and consider it best at the present time to accept *Parabyssodon* as a subgenus of *Simulium* distinct from *Byssodon*, although it must be admitted that the larva is extraordinarily closely similar to that of the African *griseicolle*-group of *Byssodon*, the larva of *transiens* having the same abdominal form and deeply divided fan-shaped setae all over the dorsum of thorax and abdomen as *griseicolle* (i.e. without the series of dorsolateral abdominal prominences and spatulate setae as occur in Holarctic *Byssodon*). The *Eusimulium*-like pupa of *Parabyssodon* with four slender gill filaments projecting forwards is different from that of any *Byssodon* species, and the dilated fore tarsus, male genital characters, and semi-shining female scutum of *Parabyssodon* are also notable differences.

Stone (1965) assigns *S. rugglesi* Nicholson & Mickel and *S. slossonae* Dyar & Shannon to subgenus *Byssodon*, but *rugglesi*, with its male ventral plate, style shape, and postgenal cleft shape is possibly closer in its characters to *Simulium* s. str.

(despite the large claw tooth of the female and unarmed cibarium) than to true *Byssodon*; I exclude it from *Byssodon* as here defined. *S. slossonae* is known to me only from description, from which I could not associate it with *meridionale*, type-species of *Byssodon*, sufficiently closely for assignment to this subgenus.

The affinities of *Byssodon* are very uncertain. Rubzov (1959-1964) places the segregate (under the name *Titanopteryx*) between *Cnephia* and *Eusimulium*, a position in his classification that implies that *Byssodon* is a rather primitive group, despite the 'advanced' character of bare base to the radius (a feature presumably evolved more than once); the simple male hypopygium and female gonapophyses, the rather fully scaled female abdomen, and slender fore tarsus recall *Eusimulium* but the cuticular covering of setae on the larva show analogy with *Edwardsellum* or *Parabyssodon*, and the divided fan-shaped setae occurring in some forms are reminiscent also of *Pomeroyellum*. Taking all the characters together it is impossible to ascribe particular affinity to any other subgenus or group of subgenera with confidence.

The subgenus includes some species that periodically form serious outbreak swarms, when biting of man and livestock becomes commonplace even though the species are as a rule ornithophilic; in this regard *Simulium* (*Byssodon*) *griseicolle* along the Nile valley in the Sudan shows closely similar behaviour to that of *S.*(*B.*) *meridionale* on the Mississippi River.

The Holarctic and Ethiopian forms of *Byssodon* fall into two distinct species-groups:—

***meridionale*-group.** Pupal gill arborescent, with 22-26 filaments. Pupal abdomen with sparse backwardly-directed spine-comb dorsally on segment 8, sometimes trace of similar comb on segment 7. Larval head with postgenal cleft broadly reaching base of hypostomium, postgenal bridge therefore obliterated, sides of cleft slightly convex. Larval abdomen with dorsolateral rows of swellings on first five or six segments, and with small subconical ventral papillae. Thoracic and abdominal cuticle with flattened slightly scale-like simple setae.

Included taxa. Palaearctic Region: *Simulium* (*Byssodon*) *heptapotamicum* Rubzov; *S.*(*B.*) *maculatum* (Meigen) including the supposed subspecies recognized by Rubzov (1959-1964: 259-262). Nearctic Region: *S.*(*B.*) *meridionale* Riley [synonyms: *occidentale* Townsend, *forbesi* Malloch].

***griseicolle*-group.** Pupal gill not arborescent, bifid or trifid with flattened lanceolate or subcylindrical or subspherical branches. Pupal abdominal segments without dorsal spine-combs. Larval head with very large subcircular postgenal cleft separated from base of hypostomium by narrow but complete postgenal bridge (Text-fig. 262). Larval abdomen without dorsolateral prominences and without definite ventral papillae. Larval thoracic and abdominal cuticle with deeply divided compound fan-shaped setae.

Included taxa. *Simulium* (*Byssodon*) *bifila* Freeman & de Meillon; *S.*(*B.*) *griseicolle* Becker; *S.*(*B.*) *tridens* Freeman & de Meillon; *S.*(*B.*) *trisphaerae* Wanson & Henrard, 1944.

Ungrouped species: *Simulium* (*Byssodon*) *buxtoni* Austen [synonyms: *bipunctatum* Austen preocc., *irakae* Smart] from Middle East, known only from female (see Crosskey, 1967b).

Subgenus *DEXOMYIA* sgen. n.

Type-species : *Simulium (Dexomyia) atlanticum* sp. n. [Description below.]

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane haired\*. Katepisternum bare. Fore tarsus slender, fore basitarsus 6.5-7 times as long as its greatest breadth. ♀ : head unusual, eyes relatively small in profile (Text-fig. 69), wide apart in dorsal view. Cibarium unarmed. Tarsal claws with large basal tooth. Scutum without definite pattern, trace of broad darker median vitta anteriorly. Abdomen evenly covered with pale hair. Seventh sternite undeveloped. Gonapophyses with slightly produced and pointed apices. Paraprocts normal. Spermatheca without internal hairs. ♂ : head normal. Scutum with bold black and greyish pattern. Genitalia with small tapering truncate styles shorter than coxites ; style with one apical spinule ; coxite not produced beyond base of style ; ventral plate lamellate and transverse with haired median keel and subparallel basal arms ; median sclerite long strap-like ; parameres long and slender, each with only one large very strong outwardly-directed parameral hook. *Pupa* : Gill with four long filaments thick at base and strongly tapering ; gill much shorter than pupal body. Abdominal onchotaxy strong and aberrant, usual four hooks each side dorsally on segments 3 and 4 but segments 5-7 ventrally with irregular transverse rows of numerous hooks, other segments dorsally and ventrally with spinous hairs or minute hooklets (total arrangement as Text-figs. 323 and 324). Cocoon shoe-shaped, with neck. *Larva* : Head and mouthparts aberrant from normal *Simulium* in several characters. Head capsule convex, cephalic apotome broadest near middle and strongly contracted on posterior half ; cephalic fans forming curved brushes, with a few exceptionally strong blackened rays completely distinct from the few finer pale rays. Hypostomium atypical, large outer prominent groups of five blunt teeth each side with deeply sunken median group of three teeth ; four or five main hypostomial setae in each row with three or four more that are much smaller, slightly irregular, rows lying subparallel to lateral margins of hypostomium. Head-spots positive, very bold. Postgenal cleft minute, an inconspicuous pointed notch, very much shorter than postgenal bridge. Mandible with blunt apical teeth, comb-teeth very strong and decreasing in size from first to third, first comb-tooth blackened and resembling apical teeth ; two mandibular serrations, sometimes apparently reduced from wear. Antenna very short, with four segments. Thoracic and abdominal cuticle toughened, strongly rugose on dorsum, abdominal segmentation exceptionally well marked by intersegmental constriction. Abdominal, and usually also thoracic, cuticle conspicuously covered dorsally and dorsolaterally with large blunt black setae admixed with smaller more spinous setae, thorax (sometimes including base of proleg) occasionally with sparse colourless hairs. Ventral papillae absent, but last abdominal segment swollen laterally. Accessory sclerites absent. Rectal scales absent. Rectal gills simple trifold, no secondary lobules. Posterior circlet with about 95-125 rows of 8-13 hooks.

Bionomy. [Oviposition habit unknown.] Larval and pupal stages non-phoretic ; attached to large loose stones in swift stream. [Female presumed able to bite, habit unknown but presumed ornithophilic.]

Distribution. St. Helena Island, South Atlantic Ocean.

Discussion. The new subgenus *Dexomyia* is erected here for a single new extraordinary aberrant species of Simuliid that occurs only on St. Helena Island in the Atlantic Ocean, and even here—despite search in many possible sites—is known from only a single stream on the southern side of the island ; the species, *Simulium (Dexomyia) atlanticum* sp. n., is fully described below, after this discussion of the unusual characteristics and possible affinities of the new subgenus.

In an earlier paper (Crosskey, 1965a) describing another species of *Simulium* from St. Helena (viz. *S. loveridgei* Crosskey) brief mention was then made of the remark-

\* or bare in ♀ (see Appendix)

able aberrant form now being described, when it was said that it would not satisfactorily fit into any of the described genera of Simuliidae. At that time only the quite unique larva and the exceptional form of pupa had been studied, the larva in particular being found to have characters apparently allying it to Prosimuliine black-flies. For the detailed study and description now given, both sexes of the adult have been dissected from mature pupae (reared or wild-caught adult flies are not yet available) and from the characters of these adults I have been forced to the conclusion that, in spite of the very atypical immature stages, the new species *atlanticum* must be placed in the genus *Simulium* sensu lato, where for a balanced classification it should form a new subgenus of its own (*Dexomyia* sgen. n.).

It has all the following adult characters of *Simulium* s.l.: Costa and  $R_1$  with spinules as well as hairs; vein  $Cu_2$  sinuous;  $R_s$  simple; no evident basal cell; calcpala and pedisulcus present; antennae 11-segmented; last segment of female maxillary palp very long and slender; male style with one apical spinule; katepisternum delimited by deep almost complete mesepisternal sulcus. In addition it shows in the pupa no long strong terminal hooks, no contorted or anchor-like apicolateral spines, and the pupal abdominal cuticle in the form of a thin transparent pellicle without brown sclerotization as in *Simulium* s.l. (i.e. without *Prosimulium*-like or *Cnephia*-like features); furthermore, the cocoon is a strongly-woven shoe-shaped pocket.

The main clue to the probable phyletic affinities of *Dexomyia* within the genus *Simulium* lies in the adult male, which (except for hairing of the pleural membrane) is virtually indistinguishable from that of *Eusimulium*. The male hypopygium (Text-fig. 311) with its keeled lamellate ventral plate and single very strong outwardly-directed parameral hook on each side is exactly of the type found in the *ruficorne*-group of Old World *Eusimulium*, and generally similar to that of *Pomeroyellum* from the African mainland. This type of hypopygium does not seem to occur in any South American segregate of *Simulium*, or in the North American fauna (although that of the *latipes*-group of *Eusimulium* there is similar) and the conclusion appears justified that *S.(D.) atlanticum* sp. n. has derived from *Eusimulium*-like forms similar to the *ruficorne*-group and reached St. Helena from the Eur-African side of the Atlantic. But although the male hypopygium is so identical with the *ruficorne*-group, perhaps indicating monophyly, this alone would not in my view justify including *atlanticum* in the subgenus *Eusimulium*, to which it will not fit on its whole constellation of characters (though there are other resemblances to *Eusimulium* in the haired base to the radius, the simple female gonapophyses, the slender fore tarsi, the very large female claw-tooth, and the four-filamented pupal gill). The subgenus *Dexomyia* is thus seen as having a closer relationship with *Eusimulium* than any other world subgenus of *Simulium*, at least more characters in common whatever the phyletic significance of this may be.

Both sexes in *Dexomyia* have the scape and pedicel segments of the antenna rather large and the flagellar segments rather loosely articulated in the manner of more 'primitive' Prosimuliine forms, and the head form of the female is also exceptional among *Simulium* species for the eyes are relatively reduced in size, so that in profile

(Text-fig. 69) they are not much wider than the postocular part of the head and in dorsal view (Text-fig. 71) are much wider apart than normal : compare with the profile and dorsal views of the female head in typical *Simulium* shown in Text-figs. 66 & 70. The female mouthparts, however, are toothed and presumably functional for haematophagy (if so, the females if anautogenous must feed on avian blood since St. Helena has no endemic mammalian fauna).

The pupal gill form in *S.(D.) atlanticum* sp. n. is in no way specially remarkable but the pupal cephalothorax is unusual among black-flies from the African area in having a covering dorsally of strong small spinous tubercles (Text-fig. 321), rather similar to those found in the subgenus *Xenosimulium* from Madagascar. The most unique feature of the pupa, however, is the presence ventrally on segments 5-7 of the abdomen of an irregular transverse row of about 14-18 strong hooks (Text-fig. 323) in place of the usual single spaced pair on each side of these segments ; the only other members of the world fauna of *Simulium* known to me to have anything similar is the mayfly-phoretic species *Simulium (Phoretomyia) lumbwanum* de Meillon from East Africa in which the fifth to seventh pupal abdominal segments are girdled with blunt black hooks (see Text-figs. 170 & 173) ; *atlanticum* does not have strong hooks dorsally on these segments, but it does have (in addition to the very reduced anterior spine-combs) two or three minute spinous-hooklets each side dorsally on the posterior margins (Text-fig. 324), another unusual feature.

The structure of the larval head in *S.(D.) atlanticum* sp. n. is superficially much more like that of Prosimuliine black-flies than that of normal *Simulium*, and the strongly bulbous sides of the head-capsule itself (Text-figs. 325 & 328) and the shape of the cephalic apotome (broadest near the middle and then contracting towards the hind margin of the head, Text-fig. 325) are just as in *Prosimulium* Roubaud, and the shape of the hypostomium in some ways resembles that found in *Stegopterna*, *Gigantodax* or even in *Gymnopais* or *Twinnia*. The resemblances to these Prosimuliine genera are, however, certainly due to convergence, for (apart from characters of the adults and pupae which confirm relationship to *Simulium* s.l. and not Prosimuliini) there are more larval characters that conform to the Simuliine and not to the Prosimuliine type ; for instance the mandible and its serrations, the very weakly developed tuft of hairs near the base of the maxillary palp, the isolated cervical sclerites, and the presence of setae on the thoracic and abdominal cuticle (which is bare in the larvae of all Prosimuliini). Another presumably convergent resemblance is that of the larval hypostomium (Text-fig. 326) to the hypostomium found in some species of the African subgenus *Phoretomyia* that attach to nymphal mayflies : there is the same tendency to formation of paired outer groups of five blunt apical teeth, with a sunken or isolated middle group of one or three teeth, as exists in the *copleyi*-group (Text-fig. 266) and the *berneri*-group (Text-fig. 267) ; furthermore *atlanticum* resembles the *copleyi*-group in the shape of the cephalic apotome (cf. Text-figs. 286 and 325) and in cranial convexity.

The cephalic fans of *Dexomyia* differ from those of all other black-flies by having the main curved rays of two distinct types, some of them slender and pale, and a few of them (usually numbering six or seven in each fan) exceptionally heavily sclero-

tized, stiff, black and strong (Text-fig. 325) ; when the fan is open the sparse large blackened rays are wide apart from each other and extraordinarily conspicuous. The strong rays give an impression under ordinary entomological binocular microscope examination of lacking the filter-apparatus, but phase-contrast examination shows that this is present and well-formed. The fans when open form shallow but convex baskets or brushes, and are not flat as in the *copleyi*-group (the only other *Simulium* segregate in the African area in which the larval mouth-brushes are strikingly modified from the normal pattern).

Attention should be drawn to one other aberrant feature of the larvae of *S. (Dexomyia) atlanticum* sp. n., the nature of the dorsal and dorsolateral parts of the thoracic and abdominal cuticle. This is strongly rugose, deeply micro-fissured with rounded or irregularly elongate raised areas between the fissuring (Text-fig. 319), the roughness being easily visible as a coarse shagreenation under low-power examination ; in addition the cuticle has a rather tough darkened appearance, is conspicuously constricted between the segments, and the segmental spiracular scars are black and obvious ; all these features, together with the vestiture of setae of diverse sizes, give the larval body a most unusual appearance. The setae cannot be looked upon as exceptional since somewhat similar ornamentation occurs in scattered species in several subgenera of *Simulium* (e.g. *Edwardsellum*, *Byssodon*, *Metomphalus*) but the shagreened cuticle appears to be unique in the Simuliidae : I know of nothing else like it in Simuliid larvae, for it is of very much coarser texture than that formed by the striations and plaque-like cuticular thickenings in the subgenus *Lewisellum*.

Included taxon. *Simulium (Dexomyia) atlanticum* sp. n.

### *Simulium (Dexomyia) atlanticum* sp. n.\*

Large species, approximate measurements : wing length 3.5-4 mm. ; pupal body length 4.5-6 mm. ; mature larval body length 9-11 mm.

♂. *Head* : Normal, holoptic, areas of enlarged upper eye facets occupying most of head and areas of lower eye facets and clypeus correspondingly reduced. Eye with about 25 rows of upper facets. Clypeus dark brown, thinly pruinose, with much long soft pale hair. Antennae 11 segmented, scape and pedicel slightly enlarged and flagellar segments not strongly compacted. Last segment of maxillary palp very elongate. Posterior surface of head normal. *Thorax* : Scutum (Text-fig. 310) with bold pattern formed by large rich velvety black median area with a broad black median vitta extending forwards to anterior margin, anterolateral corners, sides and prescutellar depression much paler grey pruinose ; in some lights trace of two fine longitudinal paler lines running through dark area and delimiting the broad black median vitta from the black areas either side ; black areas covered with dark coppery bronze scales, pale areas with silvery scales, prescutellar depression with some soft pale hair. Scutellum with long dark hair. Pleural membrane with hair, mainly on upper part, sometimes sparse. Katepisternum bare. Postnotum (postscutellum) bare. *Legs* : [Material dissected from pupae, leg colour therefore uncertain but femora except for apices and perhaps most of tibiae apparently pale.] Fore tarsus slender, fore basitarsus about six and a half or seven times as long as its greatest breadth. Hind leg with pedisulcus and with well developed calcipala ; hind basitarsus greatly enlarged, length only about three times as long as the greatest width (Text-fig. 317) or slightly less [hind tarsal curvature of pharate specimen precludes accurate statement of ratio]. *Wings* : Costa and vein

\* See Appendix for additions to description

$R_1$  with well developed spinules as well as hairs ;  $R_s$  not forked ; basal section of radius haired ;  $Cu_2$  with double curvature ; no evident basal cell ; membrane evenly covered with normal microtrichia. *Abdomen* : Sparsely haired, basal fringe long and pale ; apparently no sclerotized tenth tergite ; cerci very large and strongly sclerotized (Text-fig. 314). Hypopygium very similar in form to that found in *ruficorne*-group of subgenus *Eusimulium* (Text-fig. 311) ; styles tapering and slightly truncate at tips, shorter than coxites, with one apical spinule (Text-fig. 313) ; coxite not produced beyond base of style, hairing normal ; ventral plate (Text-fig. 312) large and lamellate, with narrow haired median keel and strongly sclerotized subparallel basal arms ; median sclerite large and elongate, slightly strap-like but each end a little wider than the middle ; parameres long and very slender, each with one very strong large (but not very elongate) parameral hook directed outwards and backwards (Text-fig. 311) ; aedeagal membrane strongly spiculate.

♀. *Head* : Atypical for *Simulium* (Text-figs. 69 & 71), eyes small so that in profile the eye-width is only a little more than the width of the postocular part of the head, in dorsal view eyes wide apart so that frons-width is almost as great as width of one eye and eye-length subequal to length of postocular part of head. Posterior surface of head blackish, frontal and clypeal regions more brownish, frons and posterior parts of head with soft recumbent pale hair, clypeus with long thick pale hair ; frons on either side with some stiffer erect slightly darker hair in addition to pale recumbent hair. Frons with trace of median furrow, especially ventrally. Antenna (Text-fig. 309) similar to male, apparently all pale. Maxillary palps very long, fifth segment slender and three times as long as the fourth segment (Text-fig. 69), sensory vesicle very small and only about one-fifth as long as its segment. Maxillae and mandibles toothed (apparently capable of biting), maxilla with 14-16 strong outer teeth and 10-12 strong inner teeth, mandibles with about 18-20 inner teeth (rather irregular) and about 8 outer teeth. *Thorax* : Scutum dark brown, trace of blacker broad median band longitudinally, especially noticeable anteriorly, humeral calli paler, scutum evenly covered with pale recumbent scales, some longer pale hair in prescutellar depression. Pleural membrane sparsely pale haired as male, katapisternum and postnotum bare as in male. *Legs* : Colouring uncertain in dissected spirit material but femora except for tips pale, and mid parts of tibiae and apparently the hind basitarsi paler than the rest. Hind basitarsus not enlarged conspicuously. Tarsal claws with large basal tooth (Text-fig. 316). *Wings* : as in male. *Abdomen* : Evenly covered with pale hair. No sternites developed basad of sternite 8. Median depression of sternite 8 strongly sclerotized. Spermatheca without surface pattern or internal hairs, spermathecal duct strongly sclerotized for short distance from point of origin from spermatheca. Gonapophyses slightly produced bluntly pointed, darkened and conspicuous (Text-fig. 315), directed backwards. Genital rod normal, lateral arms with well developed anterior process. Paraprocts normal. Cerci normal, subquadrate in lateral view but appearing to be produced to a point posterodorsally because of presence at upper angle of cluster of short stiff close-set setae standing in large-rimmed pores.

Pupa. *Head and thorax* : Closely covered dorsally with blackened pointed sharp thorny tubercles (Text-fig. 321), these largest and most strongly aggregated anteromedially on thoracic region, present but least developed on scutellar region ; trichomes simple hair-like, very inconspicuous. *Gill* (Text-fig. 322) : With four long strong tapering subequal filaments, very constant in position of branching and directional orientation : two of the filaments form a pair of basal arms of which the dorsal one curves dorsally around the pupal thorax and crosses with its fellow of the opposite side, the ventral one curving and sinuous but not bending strongly towards the opposite side ; between the basal pair the other two filaments arise and diverge very widely with scarcely any trace of common stalk, the dorsal one bending inwards and curling apically but not meeting its fellow of the opposite side, the ventral one bending and becoming sinuous or curling apically but in general direction lying parallel to the ventral filament of the basal pair ; basal part of the upper anterior filament less strongly swollen than other filaments ; all filaments transversely micro-striate along their length (as inset figure to Text-fig. 322). Whole gill very much shorter than pupal body. *Abdomen* : Aberrant, with many supernumerary hooks and spinous hooklets or hairs as detailed below, abdominal cuticle forming a thin transparent pellicle

except where lightly sclerotized and brownish dorsally on the first three or four segments and on terminal segment ; no terminal hooks, these represented by pair of conspicuous blunt black tubercles (Text-fig. 324). Onchotaxy as shown in Text-figs. 323 & 324, but variations in hook and spine numbers occur : segment 1 bare dorsally and ventrally ; segment 2 with four or five spinous hairs each side dorsally, bare or with a minute hair each side ventrally ; segment 3 with the usual four very strong hooks each side dorsally, with a spinous hair outside of these dorsally, with three or four small spinous hairs ventrally each side (of which one sometimes developed as a strong hook) and with one or two hairs laterally ; segment 4 with same armature as segment 3 except that many specimens have two strong hooks developed on each side ventrally ; segment 5 dorsally with two or three minute hairs on each side of posterior margin, ventrally with a transverse often irregular row of from 8 to 22 strong hooks and with two small spinous hairs on each side outside the hook row ; segment 6 dorsally with two small hairs each side on hind margin, ventrally with a transverse row of from 11 to 23 hooks rather irregularly arranged, normally one strong hook at each side ventrally is separated from the main row and a spinous hair present between it and main row and another laterad of the separated hook ; segment 7 dorsally bare or with two minute widely spaced hairs on hind margin, ventrally with a very irregular transverse row of from 6 to 24 hooks of which two at each end are usually separated from the main row (sometimes only one or three are separated), usually a spinous hair present in separated space at each end between the hooks, also some specimens with a spinous hair each side anteriorly and laterad of main hook row ; segment 8 dorsally usually with two widely spaced minute hairs each side on hind margin, ventrally usually bare (but one pupa seen with two strong backwardly directed hooks set wide apart on venter of segment 8). All the dorsal hooks of segments 3 and 4 and the ventral hooks of segments 5-7 simple, black and conspicuous. Fifth to eighth segments dorsally each with a transverse anterior band of microsculpture formed of minute granular or platelet-like thickenings of the cuticle (in the position where spine-combs occur in many *Simulium* pupae), the granulation produced to form an incomplete and irregular but definite spine-comb on segment 8 ; middle of each segment ventrally from segments 3-8 similarly micro-rugose, the roughening usually in paired areas (Text-fig. 323) on each segment. *Cocoon* : Very large, shoe-shaped with long neck, covering whole of pupa including the gills ; without lateral flanges or anteromedian projection, well woven but with very coarse strands visible in the texture, anterior margin rather irregular and neck area of cocoon slightly fenestrate.

*Larva. Head* : Sides of head very strongly convex, cephalic apotome broadest near the middle and thence convergent towards hind margin of head (Text-fig. 325), cephalic apotome strongly arched in profile ; head colour pale to deep honey-yellow, darker reddish brown posteriorly on cephalic apotome, with very boldly and sharply demarcated black-brown positive head-spots in which all groups are clearly isolated ; eye-spots well formed, eyebrow stripe clearly marked ; anterior part of dorsum of head transversely microstriate ; postoccipital ring black ; mandibular phragma very broad and black (Text-fig. 327) ; cervical sclerites black and isolated, very obvious. Postgenal cleft very small, very much shorter than postgenal bridge, forming a small pointed median incision in hind margin of floor of head capsule (Text-fig. 328). Hypostomium shaped as in Text-fig. 326, anterior teeth completely and extensively black, blackened area extending back to first seta in the hypostomial rows, apical teeth aggregated in two main lateral groups each with five strong blunt teeth between which is a sunken group of three teeth with the middle one strongest ; lateral margins of hypostomium with four to six strong serrations ; about 7-10 setae in each hypostomial row of which first four or five much stronger than the others, setae (especially posteriorly) rather irregular but each row lying approximately parallel to lateral edge of hypostomium. Antenna very short, not reaching end of stem of cephalic fan, third segment blackened (as in *Prosimulium* larvae) and first segment extensively pigmented dark brown especially on dorsal side, four segments and no trace of secondary annulation. Mandible (Text-fig. 330) heavily blackened and sclerotized on apical third and around the mandibular articulation, apical teeth short and blunt, first comb-tooth very large and resembling one of the apical teeth (Text-fig. 331), other comb-teeth all well developed but rather blunt, regularly decreasing in size ; two mandibular serrations, sometimes indefinite and apparently worn down to mere

irregularities on mandibular edge ; primary brush very small, not extending beyond apex of mandible. Maxilla (Text-fig. 329) with small dark palp about two and a half times as long as its basal width ; outer dorsal hair-tuft small and very inconspicuous, composed of only a few stiff colourless setae. Cephalic fans (Text-fig. 325) forming curved brushes when open, but of exceptional form, with only about 14-18 rays of two types, outer rays at each end of the series small fine and very pale but middle six or seven rays extremely large, stiff and black or brownish black, the enlarged rays very conspicuous and widely separated from each other in the opened fan ; all rays with filter-apparatus ; inner secondary fan flat and triangular when open with the tips of the rays forming a straight line (as in *Prosimulium*). Thorax : Cuticle coarsely shagreened dorsally and lightly sclerotized yellowish brown, colour appearing dark greyish laterally except for milky cervical area, proleg whitish. Bare or with a few scattered dark setae of irregular size similar to those on the abdomen ; proleg normally bare, sometimes very sparse minute simple colourless hairs near base present. Spiracular scars black, very conspicuous. Proleg plates very lightly sclerotized, with about 16 strong simple processes arising individually ; proleg circllet with about 30-40 rows of 8-12 hooks. Abdomen : Body shape normal, gradually expanding towards penultimate segment, then contracting to circllet, segmentation unusually well marked by constrictions intersegmentally, segmental spiracular scars black and very conspicuous ; colour dark brownish dorsally and pale greyish ventrally, venter milky white at junctions of segments. Cuticle with tough appearance, more or less smooth ventrally but coarsely shagreened dorsally and dorsolaterally, the microsculpture formed by deep fissuring with raised areas between the fissures, the raised areas mainly rounded dorsally (Text-fig. 319) but more elongate dorsolaterally so that these areas appear slightly striate ; cuticle in addition to shagreenation covered with dark setae on the dorsal surface, the setae conspicuous under low-power magnification and of different sizes, the large blunt setae occurring mainly on posterior half of abdomen being intermixed with smaller more spinous setae (Text-fig. 319) ; extent of distribution of setae variable, some specimens with few or none anteriorly on abdomen, others with closer cover of setae over thorax as well as abdomen, some specimens with setae extending well round sides of abdomen ; dorsolateral expansions of last segment (laterad of anal sclerite) with large long pale tapering setae. Ventral papillae absent, but sides of last segment swollen out and convex in dorsal view (Text-fig. 318). Accessory sclerites undeveloped. Rectal gills simple, each lobe bluntly rounded and without secondary lobules (Text-fig. 320), lobes milky white without pattern. Rectal scales not seen, apparently absent. Anal sclerite normal X-shape, well sclerotized. Posterior circllet with about 95-125 rows of 8-13 hooks.

Material examined. Note : the ♂ and ♀ specimens listed are pharate adults dissected from pupae and preserved in alcohol.

Holotype ♂. ST. HELENA ISLAND (SOUTH ATLANTIC) : Sandy Bay, 5.i.1963 (*A. Loveridge*). In British Museum (Natural History), London.

Paratypes\*. ST. HELENA ISLAND : 2 ♂, 2 ♀, 27 pupae, 24 larvae, Sandy Bay, 29.xii.1962 (*A. Loveridge*) ; 1 ♂, 6 pupae, Sandy Bay, 5.i.1963 (*A. Loveridge*) ; 1 pupa, 4 larvae, Sandy Bay, 10.xi.1961 (*A. Loveridge*). All paratype material in British Museum (Natural History), London, except for two larvae and two pupae deposited in United States National Museum, Washington and two larvae and two pupae deposited in Muséum National d'Histoire Naturelle, Paris.

Habitat. *Simulium (Dexomyia) atlanticum* sp. n. is so far known only from the lower reaches of a single stream on the southern side of St. Helena, where sparsely distributed larvae and pupae were found by Mr. Arthur Loveridge on large stones, sometimes in the same stretches of stream where the immature stages occur of *Simulium (Eusimulium) loveridgei* Crosskey (the only other Simuliid found on St.

\* See Appendix

Helena). Nothing is yet known of the biology of *S. atlanticum* but morphological features of the female suggest that the species is haematophagous, ornithophilic and anautogenous.

### Subgenus *EUSIMULIUM* Roubaud

*Eusimulium* Roubaud, 1906 : 521. Type-species : *Simulia aurea* Fries, 1824, by monotypy. (As subgenus of *Simulium* Latreille, 1802).

*Cnetha* Enderlein, 1921 : 199. Type-species : *Atractocera latipes* Meigen, 1804, by original designation.

*Nevermannia* Enderlein, 1921 : 199. Type-species : *Simulium annulipes* Becker, 1908 [= *Simulium ruficorne* Macquart, 1838], by original designation.

*Stilboplax* Enderlein, 1921 : 199. Type-species : *Simulium speculiventris* Enderlein, 1914, by original designation.

*Friesia* Enderlein, 1922 : 69. Type-species : *Nevermannia tristrigata* Enderlein, 1921, by original designation.

*Pseudonevermannia* Baranov, 1926 : 164. Type-species : *Atractocera latipes* Meigen, 1804, by original designation. (As subgenus of *Nevermannia* Enderlein, 1921). Junior objective synonym of *Cnetha* Enderlein, 1921.

*Chelocnetha* Enderlein, 1936a : 117. Type-species : *Chelocnetha biroi* Enderlein, 1936 [= *Simulium ornatipes* Skuse, 1890], by original designation.

*Cryptectemnia* Enderlein, 1936a : 114. Type-species : *Cryptectemnia laticox* Enderlein, 1936 [preoccupied in *Simulium* by *laticox* Enderlein, 1934, = *orsovae* Smart, 1944, replacement name], by original designation.

*Miodasia* Enderlein, 1936b : 39. Type-species : *Miodasia opalinipennis* Enderlein, 1936, by original designation.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane bare. Katepisternum bare (a few exceptions in *aureum*-group and *latipes*-group). Fore tarsus slender, fore basitarsus about 6–8 times as long as its greatest breadth. ♀ : cibarium unarmed (rarely few minute denticles). Tarsal claws almost always with very large basal tooth, rarely basal tooth small and pointed or reduced to inconspicuous blunt spinule, very rarely absent altogether. Scutum without silver-grey anterior pattern or definite dark vittae. Abdomen evenly covered with pale scales. Seventh sternite sometimes well developed. Gonapophyses simple bluntly rounded or truncate lobes. Paraprocts normal. Spermatheca often with conspicuous reticulate pattern, without internal hairs. ♂ : scutum without definite pattern. Genitalia with styles of varied form, usually broad and truncate or large and tapering and a little shorter than coxite, sometimes as long as coxite, in *aureum*-group very small in relation to coxites and with angular twist ; style with one apical spinule ; coxite not produced beyond base of style ; ventral plate not toothed, nearly always in form of large transverse plate with haired median keel and short forwardly-directed basal arms, in *aureum*-group small and elongate-triangular with very large widely divergent and outwardly directed basal arms ; median sclerite normally narrow and elongate, sometimes bifurcate with splayed ends, rarely short and broad ; parameres of varied form, usually of hinged type with one very large parameral hook and one or two small secondary hooks at base of main hook, in some forms numerous strong subequal hooks. *Pupa* : Gill usually with four long sinuous filaments directed mainly forwards, filaments sometimes divergent or thickened basally, very rarely the four filaments arising from long thick trunks, one or two of the filaments sometimes reduced thumb-like or lost completely so that gill has three filaments ; gill in some forms with 6–14 filaments ; gill typically as long as or longer than body of pupa. Abdomen with normal onchotaxy, sometimes with supernumerary pair of hooks each side ventrally on segment 4 and sometimes with row of four small hooklets each side dorsally on segment 2 ; abdominal segments 6–8 (sometimes only 7 and 8) dorsally with spine-combs. Cocoon

without neck (a few exceptions) and weakly woven, anterior margin often produced into a median dorsal process. *Larva* : Head and cephalic fans normal. Hypostomium with usual nine apical teeth, teeth usually sharply pointed and median and corner teeth prominent ; 3-7 setae in each hypostomial row, rows lying more or less parallel to lateral margin of hypostomium. Head-spots positive, usually boldly marked. Postgenal cleft typically small and subquadrate and much shorter than postgenal bridge, sometimes represented by only a slight notch or completely absent so that whole floor of head is sclerotized, in a few forms large rounded or mitre-shaped and longer than postgenal bridge. Mandible normal, second comb-tooth smaller than first or third, usually two mandibular serrations (some Holarctic forms with one or two supernumerary serrations). Antenna long and slender, normally four segments but sometimes with secondary annulations. Thoracic and abdominal cuticle usually entirely bare, occasionally with covering of minute pale hairs or with minute spinous setae posterodorsally on abdomen. Abdominal shape normal, broadest in profile at sixth or seventh segment. Ventral papillae present, usually large and subconical but sometimes small and blunt. Accessory sclerites normally absent. Rectal scales present (possibly exceptions). Rectal gills with or without secondary lobules. Posterior circlet with 60-115 (usually 65-80) rows of 9-16 (usually 10-14) hooks.

*Bionomy*. Eggs laid broadcast or clustered and adhered to substrate. Larval and pupal stages non-phoretic ; attached to varied substrates, but often small stones and dead leaves, usually in small slowly flowing watercourses but sometimes in dashing broken cascades, some forms occasionally in habitats with little or no detectable flow. Female ornithophilic.

*Distribution*. Widespread throughout North America, Eurasia and Africa, but occurring also in Central America and Australia, Madagascar and New Guinea. Occurring also in the isolated islands of Azores, St. Helena, Seychelles, Réunion, Mauritius, Rodriguez, Bonin Islands, Mariana Islands, and Caroline Islands, where (except for *Dexomyia* in St. Helena) it is the only subgenus present. Palaearctic distribution includes Iceland, Japan, North Africa and Egypt, Madeira and Canary Islands. Present in southern Arabia. Recently found in Norfolk Island.

*Discussion*. *Eusimulium* is the largest and most widely distributed subgenus of *Simulium* and the only one that can be considered almost cosmopolitan, since it is the only one that has successfully colonized the remote oceanic islands. The subgenus has an essentially Arctogaean distribution, as it is apparently absent from South America (although found in the northern Neotropical areas of Mexico and Guatemala) and in Australia is represented by only a single species : it is best developed in the Holarctic Regions, where almost forty per cent of the species of *Simulium* are assignable to subgenus *Eusimulium*. There is a much smaller *Eusimulium* fauna in the Ethiopian and Malagasy Regions, where only some twelve per cent of the species belong in the subgenus.

The place that *Eusimulium* occupies as a main component of the *Simulium* fauna in the temperate Holarctic is taken in the tropics by large endemic subgenera that appear to be related to *Eusimulium* in many of their characters, but which are best ranked as separate subgenera : these are *Pomeroyellum* in the Ethiopian Region, *Gomphostilbia* Enderlein in South-East Asia, *Morops* Enderlein in New Guinea, and *Psilopelmia* Enderlein in the Neotropical Region. The differences and resemblances between *Eusimulium* and *Pomeroyellum* are considered in detail in the discussion

section under the latter name, and those between *Eusimulium* and Oriento-Australasian subgenera *Gomphostilbia* and *Morops* have been discussed elsewhere (Crosskey, 1967a). *Eusimulium* differs from the New World segregate *Psilopelmia* by having the cibarium of the female fully or almost unarmed, by having (with few exceptions) a very large basal tooth to the claws of the female, usually by having only one very strong parameral tooth with one or two minute additional teeth, and by having positive larval head-spots: in addition the basal section of the radius is often bare in *Psilopelmia*, whereas it is always haired in *Eusimulium*.

In the African area *Eusimulium* covers a greater geographical range than any other genus or subgenus of Simuliidae, despite the relative deficiency in the number of species occurring in the Ethiopian and Malagasy Regions (Map 2); it occurs not only in tropical and southern Africa, but also from Morocco to Tunisia, in Sinai peninsula of Egypt, in South Yemen, Seychelles, Madagascar and the Mascarene islands, and in St. Helena. It is not yet known from Libya, from which no Simuliidae have been recorded, but probably occurs there. The subgenus contains the only species of Simuliidae known from the Sahara: *Simulium (Eusimulium) ruficorne* Macquart is a species adapted to survival in conditions of very reduced flow, or even no flow at all, and has been recorded from the Tibesti and Tassili des Ajjer massifs in the central Sahara.

In the Palaearctic Region the *Eusimulium* fauna has been subjected to excessive taxonomic splitting by some workers, usually on the basis of very slender morphological evidence provided by small differences in the male genitalia, and Rubzov (1959-1964) recognizes a little over one hundred species from this region; by contrast, Stone (1965) lists only twenty species from America north of Mexico (but states that *aureum* and *latipes* in this area are unrevised species complexes). Despite this great difference in the number of named entities in the Nearctic and Palaearctic areas the *Eusimulium* fauna is essentially very similar, and most of the North American species clearly fall into one or other of the seven species-groups of *Eusimulium* delimited by Rubzov for the Palaearctic Region. Three of these species-groups are clearly present in the fauna of Africa and its islands.

The most primitive forms of *Eusimulium*, or at least those showing the greatest number of characters resembling Prosimuliine black-flies, are those which lack a definite pedisulcus and have a widely spaced series of serrations on the larval mandible. These form the *annulum*-group of Rubzov (1959-1964), otherwise called the *subexcisum*-group by Davies (1966), and are not represented in the African fauna (in which all species of *Eusimulium* have the pedisulcus well developed). An unusual character in the *annulum*-group, not to be regarded as primitive, is the presence of secondary annulations on the larval antenna: this feature does not occur in the larvae of any African species.

In the North American fauna five species, *S.(E.) anatinum* Wood, *S.(E.) con-gareenarum* (Dyar and Shannon), *S.(E.) excisum* Davies, Peterson & Wood, *S.(E.) innocens* (Shewell) and *S.(E.) rivuli* Twinn, form a natural group in which the pedisulcus is very shallow, the male style long and tapering, there are many parameral teeth, the larval antenna is most often secondarily annulated, and in which

(with the exception of *rivuli*) there are more than four filaments (6, 10, or 12) in the pupal gill ; this group clearly corresponds to Rubzov's *annulum*-group, and therefore has no equivalent in the Ethiopian and Malagasy fauna. One of its species, *S.(E.) congareenarum*, is apparently very closely allied to *S.(E.) dogieli* (Ussova) from Karelia, which Rubzov (1959-1964) in his Palaearctic monograph first placed in *Eusimulium* but later (p. 591, op. cit.) transferred to the genus *Greniera* : this re-assignment, whether justified or not, emphasizes the fact that many of the more primitive Holarctic forms placed in the subgenus *Eusimulium* are so similar in many of their characteristics to certain Prosimuliine genera that it is even doubtful whether they should be placed in the genus *Simulium* at all. In the Ethiopian and Malagasy Regions such difficult intermediate forms do not occur, and the Prosimuliine and Simuliine faunas of these areas are readily differentiated.

The *batoense*-group of *Eusimulium*, delimited by Rubzov for a small number of species from Japan, contains some forms in which the katepisternum is fully haired (such as *batoense* Edwards itself) and others in which it is bare. The species showing the former character appear to have all the diagnostic features of the Oriental subgenus *Gomphostilbia*, and have been assigned to this subgenus in an earlier paper (Crosskey, 1967a : 38). The remaining Japanese species in the *batoense*-group in Rubzov's sense have a gill with four or six filaments, multiple parameral hooks, and the katepisternum bare : these species (*S.(E.) yamayaense* Ogata & Sasa, *S.(E.) mie* Ogata & Sasa, and *S.(E.) sasai* Rubzov) are assignable to *Eusimulium*, not to *Gomphostilbia*, and appear to show some affinity with *S.(E.) euryadminiculum* Davies or *S.(E.) furculatum* (Shewell) from the Nearctic Region. They also have a striking resemblance to the *loutetense*-group from the Ethiopian Region (defined below).

The African fauna contains no species that fit with the rather weakly defined *montium*-group and *alpinum*-group of Rubzov.

In the present work four species-groups are recognized for the fauna of the African area and can be distinguished by the following key.

#### KEY TO THE SPECIES-GROUPS OF *EUSIMULIUM* IN AFRICA AND ITS ISLANDS

- 1 Ventral plate of ♂ with small subtriangular body and large outwardly directed basal arms (Text-fig. 102) ; style very small in relation to coxite and with characteristic shape (Text-fig. 142). Postnotum with scale patch on either side. Cocoon simple . . . . . **aureum-group** (p. 65)
- Ventral plate of ♂ with large transverse lamellate body and small forwardly directed basal arms (Text-figs. 100, 101, 103); style large, not of this shape. Postnotum bare (except in occasional specimens of *latipes*-group). Cocoon simple or with triangular or long horn-like anteromedian process . . . . . 2
- 2 ♂ hypopygium with one very long strong parameral hook on each side (Text-fig. 88). Postgenal cleft of larva almost absent or small rounded or subquadrate, subequal in length to or much shorter than postgenal bridge (Text-figs. 241-244). Cocoon without neck . . . . . 3
- ♂ hypopygium with several (usually 3-6) parameral hooks on each side. Postgenal cleft of larva large and mitre-shaped (Text-fig. 245), very much longer than postgenal bridge. Cocoon with or without neck . . . . . **loutetense-group** (p. 63)

- 3 ♂ hypopygium with median sclerite deeply cleft Y-shaped ; style heavy and produced distally beyond level of insertion of the spinule ; paramere broad and irregular plate-like ; ventral plate without definite median keel, but with haired apical lip. Cocoon (in extra-limital forms) often with elongate median down-curved process . . . . . **latipes-group** (p. 60)
- ♂ hypopygium with median sclerite parallel-sided and rod-like, or if dilated apically not deeply cleft (except in *loveridgei*) ; style, even if broadly truncate, not noticeably produced distally beyond level of insertion of the spinule ; paramere narrow and elongate ; ventral plate with a haired median keel (Text-fig. 101). Cocoon with or without short triangular median projection but without long horn-like process . . . . . **ruficorne-group** (p. 61)

**latipes-group.** Postnotum bare (except in occasional specimens). Styles large and broad apically, produced beyond level of spinule insertion ; ventral plate large and broad, without median keel, basal arms directed forwards ; parameres in form of irregularly shaped plates each bearing one long strong parameral hook ; median sclerite characteristic, Y-shaped. Pupal gill with 4 filaments (except in North American species *croxtoni* Nicholson & Mickel and *wyomingense* Stone & DeFoliart with 8 filaments and *gouldingi* Stone with 6 filaments). Cocoon without neck, simple or with long single or paired median horn-like process. Larval antenna without secondary annulations, with or without one or two small supernumerary mandibular serrations. Larval postgenal cleft normally shorter than or subequal in length to postgenal bridge, rounded anteriorly or subquadrate, sometimes forming only a slight notch in posteroventral margin of head.

This is the predominant species-group in both the Palaearctic and Nearctic Regions ; it is absent from the Ethiopian and Malagasy Regions, but occurs in North Africa (Morocco). The group appears to be absent from most of the Oriental Region, yet is undoubtedly present in Java, where two species occur, *S.(E.) tosariense* Edwards and *S.(E.) tjibodense* Edwards, that were originally described by Edwards (1934) as varieties of *latipes* Meigen : that these taxa belong in the *latipes*-group and are very similar to European *latipes* has been confirmed while preparing the present paper from material of the type-series in the British Museum collection. In an earlier paper (Crosskey, 1967a : 33) it was suggested that no species of the *latipes*-group occur in the Old World tropics, but this overlooked the presence of the two Javanese forms mentioned above. The group is apparently not represented in the Canary Islands, although both the *aureum*-group and *ruficorne*-group occur there.

The *latipes*-group is best differentiated from all other groups by the very distinctive male hypopygium with very deeply divided median sclerite and heavy styles of a constant and unique shape : the styles are broadly truncate apically but protrude beyond the level at which the inwardly and forwardly directed spinule is inserted, and are twisted so that the apical part is bent inwards (well shown in figs. 71-74 in Davies *et al.*, 1962). The group is most closely related to the *ruficorne*-group, as discussed further below.

*S.(E.) latipes* (Meigen) itself is the type-species of Enderlein's genus *Cnetha*, of which *Pseudonevermannia* Baranov is a junior objective synonym, and if at any time the subgenus *Eusimulium* is further subdivided into named subgenera then *Cnetha* Enderlein, 1921, will be the oldest genus-group name available (other than *Nevermannia* Enderlein dating from the same publication) for the residual concept after separation of *Eusimulium* proper (i.e. the *aureum*-group, discussed below).

Included taxa. The group includes the following forms from the Regions indicated :

Palaeartic Region : all taxa assigned to the *latipes*-group in Rubzov (1959-1964), one of which occurs in North Africa : *S.(E.) costatum* Friederichs.

Nearctic Region : *S.(E.) aestivum* Davies, Peterson & Wood ; *S.(E.) bicorne* Dorogostajskij, Rubzov & Vlasenko [also in Palaeartic Region] ; *S.(E.) croxtoni* Nicholson & Mickel ; *S.(E.) gouldingi* Stone ; *S.(E.) impar* Davies, Peterson & Wood ; *S.(E.) latipes* (Meigen) [also in Palaeartic Region] ; *S.(E.) pugetense* (Dyar & Shannon) ; *S.(E.) quebecense* Twinn ; *S.(E.) wyomingense* Stone & De Foliart.

Oriental Region : *S.(E.) tjibodense* Edwards ; *S.(E.) tosariense* Edwards.

**ruficorne-group** (= *angustitarse*-group). Postnotum bare. Styles simple and bluntly truncate (Text-figs. 143 & 144) ; ventral plate large and broad, with haired median keel, basal arms directed forwards ; parameres narrow and elongate (Text-fig. 88), each bearing one long strong parameral hook (occasionally a minute supernumerary hook or spine near base of main hook) ; median sclerite elongate and rod-like or slightly clubbed, not noticeably bifurcate (except in *loveridgei*). Pupal gill with 4 or 6 filaments ; when 4 filaments present these sometimes arising from paired or single large trunk (Text-fig. 180), or one or two of them reduced thumb-like (Text-fig. 179), very rarely one lost completely so that gill may have only 3 filaments in some specimens. Cocoon simple or with subtriangular median projection (usually not long horn-like as in some *latipes*-group forms). Larval antenna without secondary annulations, larval mandible without supernumerary mandibular serrations. Larval postgenal cleft much shorter than postgenal bridge, small rounded or subquadrate, forming a minute notch in posteroventral margin of head or absent altogether (Text-figs. 242-244).

This group was termed the *ruficorne*-group by Freeman & de Meillon (1953) for the Ethiopian fauna and the *angustitarse*-group by Rubzov (1959-1964) and Davies (1966) for the Palaeartic fauna, both names applying to the same species-group concept. The name *ruficorne*-group is here preferred as this has prior usage, and *S.(E.) ruficorne* Macquart, 1838 itself occurs in both the Palaeartic and Ethiopian Regions and has the widest distribution of any included species.

The group appears not to be represented in North America, but has a wide distribution throughout the Old World that includes Europe, North Africa and Canary Islands, Middle East and southern Arabia, Central Asia, the Oriental Region, Australia, New Guinea and New Caledonia, and the whole of the Ethiopian and Malagasy Regions. It is undoubtedly closely related to the *latipes*-group, from which the immature stages on a group basis cannot be satisfactorily delimited, but differs by the distinctive male ventral plate in which there is a characteristic haired median keel (in the *latipes*-group the large broad plate has a haired down-bent lip but no definite median keel) ; the male hypopygium also differs by having long slender subparallel-sided parameres, differently-shaped styles (styles of *latipes*-group described above), and by the median sclerite not having a deep apical cleft. *S.(E.) loveridgei* from St. Helena Island, which certainly belongs in the *ruficorne*-group, is an exception for the last character as it has a Y-shaped median sclerite (Crosskey, 1965a), although the prongs of the Y are shorter and less widely splayed than those of *latipes*-group species. The *ruficorne*-group is distinguished from the *loutetense*-

group, the only other group represented in the Ethiopian Region, by the one long hook on each paramere of the male hypopygium (this is sometimes associated with one or a pair of minute supernumerary hooks at the base), by the well defined keel on the ventral plate and by the small or indefinitely developed postgenal cleft of the larva.

The *ruficorne*-group has successfully colonized several of the remote islands of the Atlantic (St. Helena) and Indian oceans (Seychelles, La Réunion, Mauritius, Rodriguez), but it is not certain how the necessary transoceanic dispersal occurred—in the case of St. Helena over at least 1200 miles from the nearest continental mainland. Carriage on birds, since the *ruficorne*-group forms like other *Eusimulium* are ornithophilic and in the female have large claw-teeth, is a possible explanation but no evidence exists that Simuliidae can survive on birds for more than a very short time.

*S.(E.) speculiventre*, the only Simuliid occurring in the Seychelles Islands, differs from typical *ruficorne*-group forms, however, by having the tooth on the claws of the female very reduced, the male ventral plate rather narrow and with more rounded posterolateral corners than usual, the suture apparently obliterated between the first two segments of the larval antennae, and by having an exceptionally high number of hooks in the posterior larval cirlet (about 140 rows of 16–19 hooks); despite these atypical features it appears best to assign *speculiventre* to the *ruficorne*-group in preference to creating a special group for an exceptional species alone. Freeman & de Meillon (1953: 64) placed the species in their *alcocki*-group of *Simulium* (now in the subgenus *Pomeroyellum*) but this was before the discovery of the immature stages; these, recently described by Crosskey (1966), clearly show that *S. speculiventre* Enderlein belongs in the subgenus *Eusimulium* and not to *Pomeroyellum*.

A second aberrant species here assigned to the *ruficorne*-group on its balance of characters is *S.(E.) starmuhlneri* from Madagascar (Grenier & Grjébine, 1963). The characters of the male hypopygium including large broad ventral plate with median keel, long narrow parameres with single large tooth, and shape of the style, conform exactly to those of *ruficorne*-group, but the female has almost no trace of a claw-tooth, the four exceptionally fine thread-like filaments of the pupal gill arise from a single large elongate trunk (Text-fig. 180), the larval abdomen shows well developed traces of a sclerotized accessory ring in front of the posterior cirlet, and the larval mandible has three mandibular serrations in place of the normal two; though the species is distinctive and atypical in the larval and pupal stages, the male hypopygial characters confirm that the affinities of *starmuhlneri* are with other members of the *ruficorne*-group.

Enderlein's generic names *Nevermannia*, *Stilboplax* and *Chelocnetha* are all based on species in the *ruficorne*-group (see synonymy of *Eusimulium* given above) and are here treated therefore as synonyms of *Eusimulium* Roubaud; they have not been in use as genus-group names in the Simuliidae for the past quarter-century, except by Japanese workers on the simuliid fauna of Japan and Ryukyu Is. who have used the names *Nevermannia* and *Stilboplax* for subgeneric segregates (Ogata,

1956 ; Ogata & Sasa, 1954, 1955 ; Shogaki, 1956). Of the several species of subgenus *Eusimulium* placed in *Stilboplax*, *Nevermannia* or *Eusimulium* by these Japanese authors only *S.(E.) aureohirtum* Brunetti belongs in the *ruficorne*-group proper as here defined ; this is an Indian species recorded from Japan by Ogata & Sasa (1955) and from the Ryukyu Islands by Ogata (1956), but possibly misidentified from Japan.

Included taxa. The group includes the following taxa from the regions indicated :—

Ethiopian Region : *S.(E.) aureosimile* Pomeroy ; *S.(E.) buckleyi* de Meillon ; *S.(E.) duboisi* Fain ; *S.(E.) fuscicorne* Fain ; *S.(E.) katangae* Fain ; *S.(E.) loveridgei* Crosskey [St. Helena Island] ; *S.(E.) nigrিতarse* Coquillett ; *S.(E.) ruficorne* Macquart [also Palaearctic and Malagasy Regions].

Malagasy Region : *S.(E.) speculiventre* Enderlein [Seychelles] ; *S.(E.) starmuhlneri* Grenier & Grjébine [Madagascar].

Palaearctic Region : *S.(E.) angustitarse* (Lundström) ; *S.(E.) crassicaulum* (Rubzov) ; *S.(E.) delizhanense* (Rubzov) ; *S.(E.) flavipes* Austen (= *jerichoense* Smart, invalid replacement name) ; *S.(E.) latigonium* (Rubzov) ; *S.(E.) lundstroemi* (Enderlein) ; *S.(E.) montshadskii* (Rubzov) ; *S.(E.) subgriseum* Rubzov ; *S.(E.) vitile* (Rubzov).

Oriental Region : *S.(E.) aureohirtum* Brunetti. [Probably also *S.(E.) geniculare* (Shiraki) from Formosa (type-locality) and Japan].

Australasian Region : *S.(E.) ornatipes* Skuse (syn. *biroi* Enderlein).

[Note : *Simulium irakae* Smart (= *buxtoni* Austen) from the Middle East belongs in the subgenus *Byssodon* Enderlein and is wrongly placed by Rubzov (1959–1964 : 359) in his *angustitarse*-group of *Eusimulium*.]

***loutetense*-group.** Postnotum bare. Styles simple and rounded-truncate, moderately large, not noticeably produced beyond level of spinule insertion ; ventral plate large and broad, without narrow median keel but usually with large slightly down-turned haired lip (Text-fig. 103), basal arms small and directed forwards ; parameres narrow, parameral hooks large and multiple, normally 3–7 on each side ; median sclerite broad rod-like or bifurcate apically, if the latter normally with thinly sclerotized area connecting the arms. Pupal gill with 4, 6 or 8 filaments, long and slender (if 8 arising 3+3+2). Cocoon simple or with loosely woven neck, without horn-like projection. Larval antenna without secondary annulations, larval mandible without supernumerary mandibular serrations. Larval postgenal cleft (where known) large and pointed mitre-shape (Text-fig. 245), much longer than postgenal bridge. Larval abdomen with sparse minute colourless hairs and with the ventral papillae in form of rather ridge-like swelling mainly ventrolateral in position.

This group is proposed for three Ethiopian species that Freeman & de Meillon (1953 : 162–167) placed in the *dentulosum*-group of Division B in their classification of Ethiopian *Simulium*, but which appear without doubt to be assignable to the subgenus *Eusimulium* (not to subgenus *Anasolen* that contains the *dentulosum*-group proper). Freeman & de Meillon assigned these species (*loutetense*, *rutherfordi* and *narcaeum*) to Division B because of the multiple parameral hooks in the male hypopygium, although the female terminalia, filamentous gill with 4 or 6 filaments, and the dorsal spine-combs on segments 6–8 (sometimes not 6) of the

pupal abdomen are all characters conforming with their Division A groups. Considering the characters of both sexes and all stages together it seems certain that the affinities of these Ethiopian species lie with those forms of *Eusimulium* from other regions that have multiple parameral hooks, a large transverse male ventral plate without median keel, simple male styles, four or six pupal gill filaments, and no secondary annulation on the larval antenna, and they are here placed without hesitation in the subgenus *Eusimulium*. It should be noted, however, that the larval stage is known only of *loutetense* and the larval group characters cited in the foregoing group definition may need modifying when larvae of *rutherfordi* and *narcaeum* are available.

The Holarctic forms of *Eusimulium* in which there are many parameral hooks in the parameral organ of the male hypopygium do not group so readily as those in which there is one large main hook (*latipes*-group, *ruficorne*-group, *aureum*-group), and a satisfactory group treatment for them has not yet been worked out: instead of fitting the Ethiopian species to one of the named Holarctic groups, therefore, a group is here proposed and defined for them with *loutetense* as lead species. One North American species, *S.(E.) furculatum* (Shewell), however agrees so well with *loutetense* and the definition of the *loutetense*-group that it is here assigned to the group.

*S.(E.) furculatum* differs from *S.(E.) loutetense* by having a simple non-necked cocoon and an 8-filamented (instead of 6-filamented) gill, but in all other characters shows an extraordinarily close agreement. The females of the two species have the claw-tooth minute or virtually absent (an uncommon condition among *Eusimulium* species), and the larvae of both have a very similar large mitre-shaped postgenal cleft (Text-fig. 245) and unusually bold head-spot pigmentation. The larval abdomen is unusual amongst species of *Eusimulium* but is similar in the two species: the ventral papillae are small and bluntly rounded in profile, rather inconspicuous, but are represented by a slightly swollen ridge in a more lateral position than normal (i.e. not downwardly directed and subconical as in typical members of the subgenus), and the cuticle is sparsely covered with minute colourless hairs. The agreement in unusual characters is so close that true phyletic affinity probably exists.

In the Oriental Region and Japan several species occur that, to judge from the figures and descriptions, are closely similar to the species from Africa here forming the *loutetense*-group. The evidence is not sufficient at present to assign these species positively to the group, but attention is drawn to them here as the Ethiopian species very likely have rather close affinity with at least some of them: the species referred to are *S.(E.) mie* Ogata & Sasa, *S.(E.) yamayaense* Ogata & Sasa, and *S.(E.) sasai* Rubzov from Japan, *S.(E.) philippinense* Delfinado from the Philippines and *S.(E.) rufithorax* Brunetti from India. The male genitalia of *Simulium feuerborni* Edwards and *S. fuscinervis* Edwards, together with other characters so far as known, resemble those of the *loutetense*-group, but in these Indo-Malayan species the fore tarsus is quite exceptionally slender and it is not certain that they are assignable to *Eusimulium* at all.

The Japanese species aforementioned have been placed by Rubzov (1959-1964 : 308-312) in his *batoense*-group of *Eusimulium*, but *batoense* Edwards has the characters of the subgenus *Gomphostilbia*, a weakly-defined subgenus near to *Eusimulium* but considered distinct in an earlier paper (Crosskey, 1967a). In that paper, the three Japanese species in which the katepisternum is haired and the pupal gill has eight filaments, viz. *S.(G.) omutaense* Ogata & Sasa, *S.(G.) shogakii* (Rubzov) and *S.(G.) ogatai* (Rubzov), were removed from *Eusimulium* and placed in *Gomphostilbia*, where it is here considered that they should be assigned ; but the other three Japanese species in Rubzov's *batoense*-group (*mie*, *yamayaense* and *sasai* mentioned above) have the katepisternum bare and 4 or 6 filaments in the pupal gill, and these remain best placed in *Eusimulium* near to the *loutetense*-group as here defined. Nevertheless it must be recognized that those forms of *Eusimulium* with many parameral hooks, with six or eight gill filaments, and with a large pointed larval postgenal cleft, approach closely to those forms placed in *Gomphostilbia* and that their characters are intermediate between those of typical *Eusimulium* and *Gomphostilbia*. It would be possible to widen the definition of *Eusimulium*, sink *Gomphostilbia* in synonymy, and treat the species now placed in *Gomphostilbia* as a species-group of *Eusimulium*, but *Eusimulium* is more discretely defined if the *Gomphostilbia* segregate is excluded : it is here preferred to treat *Gomphostilbia* as a valid subgenus close to *Eusimulium*, showing possible affinity with the *loutetense*-group.

The two Ethiopian species (*rutherfordi* and *narcaeum*) placed in the same group with *loutetense* have the female claw-tooth strongly developed (as do the Japanese species cited above), whereas in *loutetense* itself the claw-tooth is extremely reduced : the size of the claw-tooth is not used as a diagnostic character for the *loutetense*-group. Furthermore these two species have the pupal gill with four filaments and the cocoon a simple pocket without trace of neck, the pupal stage thus closely resembling the *ruficorne*-group. The spermatheca of the female in all three species has a hexagonal reticulate pattern, as normal in subgenus *Eusimulium*.

The *loutetense*-group is unknown from the Malagasy Region.

Included taxa. Ethiopian Region : *S.(E.) loutetense* Grenier & Ovazza ; *S.(E.) narcaeum* de Meillon ; *S.(E.) rutherfordi* de Meillon. Nearctic Region : *S.(E.) furculatum* (Shewell).

**aureum-group.** Postnotum with patch of scales on each side. Style very small in relation to coxite, constricted and twisted (Text-fig. 142) ; ventral plate not lamellate, with small subtriangular body and very large widely divergent and outwardly directed basal arms (Text-fig. 102) ; parameres long and narrow, with one long strong parameral hook ; median sclerite in form of very long slender rod, sometimes frayed at tip. Pupal gill with 4 filaments, long and slender. Cocoon a simple pocket without anteromedian projection. Larval antenna without secondary annulations, larval mandible without supernumerary serrations. Larval postgenal cleft small and quadrate, much shorter than postgenal bridge.

*Simulium (Eusimulium) aureum* Fries is type-species of *Eusimulium* and this discrete and very uniform group is nomenclaturally the typical species-group in subgenus *Eusimulium*. The males of *aureum*-group species are, however, somewhat

unrepresentative of the forms currently included in *Eusimulium* as a whole because of the unique form of hypopygium, which is one of the most characteristic among all Simuliidae: the coxites and styles and ventral plate (Text-figs. 102, 142) differ strikingly from those of other species-groups of *Eusimulium*, and forms that are at all similar for these structures occur elsewhere only in the Palaearctic subgenus *Wilhelmia*. Despite this resemblance it is not likely that there is close phyletic relationship between *Eusimulium* and *Wilhelmia*.

The *aureum*-group is an entirely Holarctic segregate, absent from the Ethiopian, Malagasy, and Oriento-Australasian Regions; in the New World distribution extends southwards into Mexico and Guatemala, and the group therefore just reaches into the northern fringe of the Neotropical Region. The Palaearctic distribution includes Iceland, Canary Islands, North Africa and Middle East but the group is apparently absent from Japan (no *aureum*-group species are recorded from Japan by Ogata & Sasa, 1954; or by Rubzov, 1959-1964). On the African continent the group occurs from Morocco to Tunisia.

Rubzov (1959-1964: 365-382) has treated the Palaearctic species of the group, but has omitted the names of several supposed species of the group that have been described from the Canary Islands (see below). *S.(E.) aureum*, with some supposed synonyms, is the only species of the group in the Nearctic Region, but the name as used in North American literature refers to an unrevised species complex (Stone, 1965: 185).

Included taxa. The included taxa for the African area are:—

Canary Islands: *S.(E.) guimari* Becker; *S.(E.) nigripes* (Santos Abreu); *S.(E.) pseudolatipes* (Santos Abreu); *S.(E.) submorsitans* Séguy; *S.(E.) velutinum* (Santos Abreu). [Note: Some or all of these names are almost certainly synonyms of each other. Simuliidae of the Canary Islands need revision after collection of the immature stages and study of associated adults.]

North Africa: *S.(E.) aureum* Fries; *S.(E.) latinum* (Rubzov). [Note: Rivosecchi (1963: 210) found only *latinum* represented in North African material of the *aureum*-group and records of *aureum* from the area may be due to mis-identification.]

### Subgenus **POMEROYELLUM** Rubzov

*Pomeroyellum* Rubzov, 1962: 1492. Type-species: *Simulium cervicornutum* Pomeroy, 1920, by original designation.

Diagnosis. ♂♀: Basal section of radius haired. Pleural membrane bare. Katepisternum bare. Fore tarsus slender or at most very slightly dilated, fore basitarsus 5-7 times as long as its greatest breadth. ♀: cibarium unarmed. Tarsal claws with large basal tooth. Scutum without conspicuous pattern. Abdomen usually bare and semi-shining on last few segments, sometimes evenly covered with pale scales. Seventh sternite usually well developed. Gonapophyses simple bluntly rounded or truncate lobes. Paraprocts normal. Spermatheca without definite surface pattern or internal hairs. ♂: scutum without bold pattern. Genitalia with styles simple, tapering or bluntly truncate, shorter than or subequal in length to coxite; style with one apical spinule; coxite not produced beyond base of style; ventral plate not toothed,

of varied form, subtriangular or a broad transverse plate, with or without well developed shoulders, basal arms short and directed forwards; median sclerite simple rod-like, sometimes dilated apically; parameres long and slender, each with one very long scythe-shaped parameral hook and usually one or two much smaller hooks arising from base of main one. *Pupa*: Gill of very varied forms, filamentous or with antler-like or sausage-like branches variously modified, when filamentous not less than seven filaments in each gill; gill as long as or shorter than body of pupa. Abdominal onchotaxy normal, sometimes one or a pair of minute supernumerary hooklets each side ventrally on segment 4 and sometimes row of minute hooklets each side dorsally on segment 2; abdominal segments 7 and 8 (sometimes also 6 or 9) dorsally with spine-combs. Cocoon without neck (except in *kenyae*), sometimes with short median dorsal projection. *Larva*: Head and cephalic fans normal. Hypostomium with usual nine apical teeth, these usually sharp-pointed and median and corner teeth prominent; hypostomial setae 3-5 in each row, rows lying parallel to lateral margin of hypostomium. Head-spots negative, on cephalic apotome usually surrounded by dark pigmentation forming H-shaped mark (Text-figs. 232-234). Postgenal cleft of medium size or large, equal in length to or much longer than postgenal bridge, rounded, helmet-shaped or mitre-shaped. Mandible normal, second comb-tooth smaller than first or third; two mandibular serrations without supernumeraries. Antenna long and slender, with four segments. Thoracic cuticle bare or with minute colourless setae. Abdominal cuticle posterodorsally with small divided fan-like setae or large spatulate setae, bare in a few forms. Abdominal shape normal, broadest in profile at sixth or seventh segment. Ventral papillae present. Accessory sclerites present or absent. Rectal scales present. Rectal gills usually with secondary lobules, sometimes one or all lobes simple. Posterior circlet with 60-85 rows of 8-16 hooks.

**Bionomy.** Eggs clustered, adhered to substrate. Larval and pupal stages non-phoretic; attached mainly to dead leaves and trailing roots and grasses in slowly-flowing waters of small streams, occasionally in rapids of larger rivers or in swift cascades. Female ornithophilic.

**Distribution.** Widespread throughout the Ethiopian Region, excluding southern Arabia (Map 3), and occurring also in Madagascar.

**Discussion.** *Pomeroyellum* is the largest endemic Ethiopian subgenus, containing about thirty per cent of the species and forms of *Simulium* s.l. from the region. The segregate appears to be rather closely allied to *Eusimulium*; in fact it is difficult to separate the males of *Eusimulium* and *Pomeroyellum* by a completely satisfactory diagnosis, and the females of those forms of *Pomeroyellum* in which the abdomen is evenly covered with pale scales are indistinguishable subgenerically from *Eusimulium*. The two subgenera are most clearly separated on characters of the larva: the larvae of *Pomeroyellum* have a negative head pattern of pale spots surrounded or separated by dark infuscation (Text-figs. 232-234), and the dorsal abdominal cuticle is almost always armed with divided fan-like or large scale-like setae (Text-figs. 224 & 225); in *Eusimulium* the larval head-spots are always positive (Text-figs. 235 & 236), and the abdominal cuticle is almost always bare but occasionally has minute simple colourless hairs. In the pupal stage of *Pomeroyellum* the gill, if of the filamentous type, never has less than seven filaments, whereas four or six filaments are found in Ethiopian forms of *Eusimulium* (though eight or more occur in some Holarctic *Eusimulium*) and the cocoon in *Pomeroyellum* never has a very long horn-like median process like that of many *Eusimulium* species. The range of pupal gill form in *Pomeroyellum* includes non-filamentous shapes (Text-figs. 187-192) such as

never occur in *Eusimulium*. A characteristic feature of the females of most *Pomeroyellum* species is the reduction of pale scaling dorsally on the last few abdominal segments, so that these appear rather bare, dark and shining : in this character the subgenus resembles the Oriental subgenus *Gomphostilbia* Enderlein, but *Pomeroyellum* differs from *Gomphostilbia* by having the katepisternum bare, reduced number of parameral hooks, by the negative larval head-spots and the presence of divided or scale-like setae on the larval abdomen, and it is unlikely that there is any close phyletic relationship although *Gomphostilbia* and *Pomeroyellum* clearly belong in the same general group of subgenera.

*Pomeroyellum* may have some relationship with the subgenus *Morops* that is the predominant component of the *Simulium* fauna in New Guinea and Australia. Both subgenera include small forms with haired base to the radius, similar coxites and styles, simple haired ventral plate, filamentous gills, dorsal spine-combs on seventh and eighth pupal abdominal segments, and simple cocoons ; but *Pomeroyellum* differs from *Morops* by having the pleural membrane and katepisternum bare (both haired in *Morops*), by having one or more long strong parameral hook each side in the male hypopygium (parameral hooks virtually absent in *Morops*), and by the large female claw-tooth (absent or minute in *Morops*).

The segregate of *Simulium* in the New World most closely resembling *Pomeroyellum* is the subgenus *Psilopelmia* from Central and South America. Both subgenera have slender fore tarsi, bare pleural membrane and katepisternum, essentially similar male genitalia with similar range of form in the ventral plate, more or less similar forms of filamentous or stoutly branched pupal gills, spine-combs dorsally on the last few pupal abdominal segments, similar forms of cocoon, larvae with negative head-spots and normally with well developed ventral papillae. The main differences between *Pomeroyellum* and *Psilopelmia* are as follows :

Subgenus <i>POMEROYELLUM</i> (Ethiopian Region)	Subgenus <i>PSILOPELMIA</i> (Neotropical Region)
Cibarium unarmed	Cibarium armed with many small pointed teeth between cornuae (some exceptions)
♀ claw-tooth large	♀ claw-tooth small or absent
♂ paramere with one main hook and one or two smaller hooks	♂ parameral hooks numerous
Basal section of radius haired	Basal section of radius bare or haired
Thorax dark, without definite pattern	Thorax often orange-coloured or scutum with bold pattern
♀ paraprocts normal	♀ paraprocts normally with lower margin produced downwards, often to fine attenuate point
♀ gonapophyses bluntly rounded, not produced	♀ gonapophyses normally produced as long narrow flaps

It is probable that *Pomeroyellum* and *Psilopelmia* evolved independently from *Eusimulium*-like forms ; the latter subgenus may be looked upon as the equivalent group in the Neotropical Region to *Pomeroyellum* in tropical Africa. Both subgenera form predominant elements in their respective faunas and tend to occupy the warmer lowland streams. In Africa, *Pomeroyellum* is the main slow-water component of the black-fly fauna and forms the counterpart in slow streams to the main endemic Ethiopian subgenus *Metomphalus* found in the swift broken or cascading streams.

The species of *Pomeroyellum* fall into several distinct groups, principally on characters of the immature stages. The groups here recognized are keyed and defined below.

KEY TO THE SPECIES-GROUPS OF THE SUBGENUS *POMEROYELLUM*

- 1 Hind basitarsus of ♂ greatly dilated, only about 2.8 times as long as its greatest breadth. Cocoon with neck. Pupal gill with eight filaments arising near base in regular pairs (Text-fig. 184). Larval postgenal cleft with flattened-cordate shape (Text-fig. 249) . . . . . **kenyae-group** (p. 73)
  - Hind basitarsus of ♂ normal, not dilated and about six times as long as its greatest breadth. Cocoon without neck. Pupal gill and larval postgenal cleft of different form . . . . . 2
  - 2 Larval cuticle bare. Pupal gill formed of a single long forwardly directed tube divided apically into eight small thread-like filaments (Text-fig. 181) or with a single long recurved wrinkled tube (Freeman & de Meillon, 1953, fig. 23e). Style small relative to coxite and wide at base (Text-fig. 141) . . . . . **bequaerti-group** (p. 69)
  - Larval cuticle with divided setae or scales posterodorsally on abdomen. Pupal gill not of these forms. Style larger in relation to coxite and longer and narrower (Text-fig. 140) . . . . . 3
  - 3 Larval abdomen with large conspicuous erect scale-like setae (Text-figs. 224 & 225(a)) and with accessory sclerite on each side of last segment. Larval postgenal cleft large and mitre-shaped (Text-fig. 248) or bluntly sagittate, much longer than postgenal bridge. ♂ ventral plate pinched-in or at least slightly constricted laterally and with posterolateral 'shoulders' (Text-fig. 99). Pupal gill usually not filamentous, if so then eight filaments arising from long common stalk . . . . . 4
  - Larval abdomen with small inconspicuous semi-recumbent divided setae, usually fan-shaped (Text-fig. 225(b, c)) and without accessory sclerites. Postgenal cleft smaller and rounded or helmet-shaped (Text-figs. 246 & 247), subequal in length to or shorter than postgenal bridge. ♂ ventral plate of varied shape but not excavate laterally and therefore without posterolateral 'shoulders' (Text-figs. 96-98). Pupal gill filamentous and with 7-20 filaments, sometimes arising from common stem or trunk, if eight then not on common stem . . . . . **alcocki-group** (p. 70)
  - 4 Pupal gill filamentous, eight filaments arising from long common stem (Text-fig. 185) . . . . . **schoutedeni-group** (p. 71)
  - Pupal gill not filamentous, of varied form (Text-figs. 187-192) **cervicornutum-group** (p. 72)
- bequaerti-group.** ♂ hind basitarsus normal, slender ; style short and broad at base, small in relation to coxite ; ventral plate not noticeably excavate laterally, without definite shoulders, slender in profile. Pupal gill with one long slender undivided filament or with a very long filament branched into eight at apex. Cocoon without neck. Larval cuticle bare, abdomen without accessory sclerites. Larval postgenal cleft subquadrate or helmet-shaped (Text-fig. 247), subequal in length to postgenal bridge.

This small group differs from all other *Pomeroyellum* for which the larval stage is known by having the larval cuticle entirely bare and thus resembling that in subgenus *Eusimulium*; the head-spots, however, appear to be negative (although only poorly preserved material has been seen) and the male, female and pupal characters are also those of *Pomeroyellum* so that assignment to this subgenus is best. The style of the male is unusual as it is notably shorter and broader basally than in other species-groups and thus appears rather small when compared to the coxite. The pupal gill of *harrisoni* (figured by Freeman & de Meillon, 1953 : 86), formed by a single long wrinkled tube curved round to the opposite side of the pupal body and back towards the abdomen, is very exceptional and I know of no similar gill in any other species of Simuliidae.

Included taxa. *Simulium* (*Pomeroyellum*) *bequaerti* Gibbins; *S.(P.) harrisoni* Freeman & de Meillon.

**alcocki-group.** ♂ hind basitarsus normal, slender; styles normal; ventral plate not constricted or noticeably excavate laterally, body of plate sometimes subtriangular without prominent posterolateral shoulders, narrow and slightly curved in profile (Text-figs. 120 & 121). Pupal gill of filamentous type with from 7–20 filaments variously arising (but *not* with 8 filaments arising from end of common stem, cf. *schoutedeni*-group). Cocoon without neck. Larval abdomen with divided setae, bifid or compound and fan-like, small and usually more or less recumbent; accessory sclerites absent. Larval postgenal cleft of medium size, subequal in length to postgenal bridge, subquadrate or rounded (usually much as in Text-fig. 246).

The *alcocki*-group as here defined corresponds in the main with the group treated under this name by Freeman & de Meillon (1953), but in a slightly more restricted sense, since the *bequaerti*-group, *schoutedeni*-group and *S.(P.) kenyae* are here excluded. Freeman & de Meillon (op. cit. : 64) placed *Simulium speculiventre* Enderlein from the Seychelles in their *alcocki*-group, but as shown elsewhere in this paper *speculiventre* is actually a species of *Eusimulium*; no species of subgenus *Pomeroyellum* are known from any of the small islands of the Indian Ocean. The group includes more species and forms of doubtful taxonomic status than the other species-groups of *Pomeroyellum*, and many of the species are found rather sparsely as immature stages, attached mainly to dead leaves in small slowly-moving streams throughout lowland Africa.

Most species in the female have the posterior part of the abdomen rather bare and shining, as is typical for the whole subgenus, but in *S.(P.) merops* de Meillon and *S.(P.) evillense* Fain, Hallot & Bafort the whole abdomen of the female is thickly covered with silvery scales (recalling *Eusimulium*, in which most females show an even abdominal covering vestiture); despite this feature, *merops* and *evillense* are assigned to the *alcocki*-group on balance of characters from the male or pupa, but it should be noted that the larvae of these two species are unfortunately still unknown (and could show characters that conflict with the definition of the group given above).

The taxa in the *alcocki*-group in which there is a 10-filamented gill form a difficult complex taxonomically that probably contains several sibling or semi-sibling species showing differences only in very minor detail of the male genitalia or exact branching

arrangement of the gill. One species of this complex, *S.(P.) impukane* de Meillon, however appears to differ from others so far known by having the posterior corners of the male ventral plate prominent and by the presence of a strongly bent medio-apical lip to the plate (figured by Freeman & de Meillon, 1953 : 73). The plate of *impukane* could be described as having 'shoulders' but the sides of the plate are not pinched-in or excavated as in the *cervicornutum*-group or the *kenyae*-group.

Most species of the *alcocki*-group, like those of the *schoutedeni*-group and the *cervicornutum*-group, have rather pale legs in which the femora and tibiae are dark at the apices and the hind tibiae have in addition a sub-basal dark band (well shown in the figures of Freeman & de Meillon, 1953) ; it should be noticed, however, that in *S.(P.) merops* and *S.(P.) evillense* the legs are rather uniformly dark brown and that in this respect (as well as in the vestiture of the female abdomen mentioned above) these two species are atypical for *Pomeroyellum*.

An unusual pupal gill form occurs in *S.(P.) schwetzi* Wanson (Text-fig. 186) where the seven main filaments are swollen along their length into a sausage-form, the swollen parts having one or a pair of short terminal thread-like filaments to make up ten filaments in all. The species is only known from the pupa, but since the gill appears to be a modification from the 10-filament form found in the gill of many *alcocki*-group forms it is best placed in this group, pending confirmation of this position from the other stages when they become known.

Included taxa. *Simulium (Pomeroyellum) alcocki* Pomeroy ; *S.(P.) allaeri* Wanson ; *S.(P.) coalitum* Pomeroy ; *S.(P.) djallonense* Roubaud & Grenier ; *S.(P.) duodecimum* Gibbins ; *S.(P.) evillense* Fain, Hallot & Bafort ; *S.(P.) garmsi* **nom. n.** (= *occidentale* Freeman & de Meillon, preoccupied) ; *S.(P.) geigy* Garms & Häusermann ; *S.(P.) gilleti* Fain & Hallot ; *S.(P.) hissetteum* Gibbins ; *S.(P.) impukane* de Meillon ; *S.(P.) ituriense* Fain ; *S.(P.) johanna* Wanson ; *S.(P.) merops* de Meillon ; *S.(P.) rodhaini* Fain ; *S.(P.) schwetzi* Wanson ; *S.(P.) tentaculum* Gibbins ; *S.(P.) weyeri* Garms & Häusermann.

In addition the nomenclaturally unavailable form name *sextumdecimum* has been applied by Luna de Carvalho (1962) to a taxon of this group.

**schoutedeni-group.** ♂ hind basitarsus normal, slender ; styles normal ; ventral plate excavate laterally near base of basal arms or with a lateral notch each side in ventral view, shoulders well developed, rather thickened in profile. Pupal gill of filamentous type, eight filaments arising from long common stem. Cocoon without neck. Larval abdomen with sparse very large erect flattened scale-like setae, mainly dark and conspicuous, and with accessory sclerites. Larval postgenal cleft large and much longer than postgenal bridge, broadly and bluntly sagittate in shape.

This small group, containing only two species at present, is completely intermediate between the *alcocki*-group and the *cervicornutum*-group, showing a filamentous type of pupal gill like the former but a larval stage with large flat abdominal scales, accessory sclerites, and postgenal cleft like the latter group. On the basis of the larvae the two species—if no other stages were known—would be immediately placed in *cervicornutum*-group, whereas if the larvae were unknown they would fit the *alcocki*-group on pupal characters ; if the two species were placed in either of these

groups it would make the resultant group much less homogeneous and more difficult to diagnose satisfactorily. They are therefore placed here as a small group of their own, coming between the *alcocki*-group and the *cervicornutum*-group. The existence of this intermediate group, with larvae like those of *cervicornutum* but pupae like the *alcocki*-group, confirms that—despite the striking difference in pupal gill form—the *alcocki*-group and the *cervicornutum*-group should be treated as consubgeneric ; the *alcocki*-group is therefore assignable to subgenus *Pomeroyellum*.

The form of the male ventral plate in the species of *schoutedeni*-group is slightly closer to that in *cervicornutum*-group than *alcocki*-group.

Included taxa. *Simulium* (*Pomeroyellum*) *mcmahoni* de Meillon ; *S.(P.) schoutedeni* Wanson.

***cervicornutum*-group.** ♂ hind basitarsus normal, slender ; styles normal ; ventral plate with well developed shoulders, excavate laterally (Text-fig. 99), slender or slightly thickened in profile. Pupal gill not filamentous, of large bladder-like or branched antler-like form variously modified (Text-figs. 187–192). Cocoon without neck. Larval abdomen with large sparse erect scale-like setae, dark and conspicuous, and with accessory sclerites. Larval postgenal cleft large and much longer than postgenal bridge, mitre-shaped.

*S.(P.) cervicornutum* Pomeroy is type-species of *Pomeroyellum* and this is the typical group of the subgenus nomenclaturally ; it contains all the species of *Pomeroyellum* in which the pupal gill is not of the filamentous type. The group is widespread in the Ethiopian Region and one species, *S.(P.) pauliani* Grenier & Doucet, is found in Madagascar. The *cervicornutum*-group, more than any other group of *Pomeroyellum*, is adapted to live in a variety of fluvial habitats from slowly-flowing weedy streams to broken fast waters in large rivers, occasionally even in mountain cascades, and the immature stages of *cervicornutum* itself may be found in a wider variety of situations than those of any other Ethiopian Simuliid ; even *unicornutum* Pomeroy, although habitually occupying small-stream habitats, sometimes occurs in the rapids of large rivers.

The larvae of the group can be recognized at once among mixed collections of black-fly larvae from the Ethiopian Region by the characteristic large blackened and erect scales standing sparsely on the posterodorsal part of the abdominal cuticle, and readily seen with low-power magnification. Apart from similar vestiture in larvae of the related *schoutedeni*-group (see above), such arrangement of large sparse scales appears to be unique among the larvae of world *Simulium*. In addition to the scales, the abdomen of *cervicornutum*-group larvae is rather distinctive because of the presence of a pair of small accessory sclerites (one each side of the last segment immediately before the cirlet : Text-fig. 224) and of an unusually dark annular mottling on the segments ; in addition the mediodorsal parts of the first four or five segments are often rather prominent (sometimes even tending towards the development of tubercles recalling those of *Edwardsellum* larvae).

The pupal gill in this group assumes a variety of forms that is probably more diverse than in any other segregate of Simuliidae, with the possible exception of the Nearctic and northern Neotropical subgenus *Hearlea* Vargas, Martinez Palacios & Diaz Najera in which a somewhat similar bizarre range of form occurs (figured, for

instance, by Dalmat, 1955 ; Vargas & Diaz Najera, 1957). Some of the gill forms in *Hearlea* tend to resemble those of *S.(P.) cervicornutum*, while others resemble forms near *S.(P.) unicornutum*, but having regard to all the characters of *Hearlea* it seems certain that the resemblances are due to convergence ; close phyletic affinity between *Hearlea* and *Pomeroyellum* appears very unlikely. The gill in the *cervicornutum*-group species falls into two main types ; firstly, those like *unicornutum* in which a thin-walled bladder-like gill is variously modified into barrel or sausage-like (Text-figs. 190 & 192) form or takes on an almost amoeboid outline (Text-fig. 189), and, secondly, the type of antler-like gill (Text-fig. 187) of *cervicornutum* that may be a development from a gill with more stunted less definite branches (Text-fig. 188). Until recently these two types of pupal gill in the *cervicornutum*-group were rather distinct, but the discovery of *S.(P.) leberrei* with its curious form of pupal gill (Text-fig. 191, redrawn from Grenier, Germain & Mouchet, 1965*b*) tends to bridge the gap in form between the two types (although the nature of the *leberrei* gill is closer to the *unicornutum* type than the *cervicornutum* type).

There is a resemblance in the type of large inflated or irregularly branched gill in some *cervicornutum*-group forms to the pupal gills of *Simulium botulibranchium* Lutz from Brazil (figured by d'Andretta & d'Andretta, 1947) and of *Paraustrosimulium anthracinum* (Bigot) from Tierra del Fuego (figured by Wygodzinsky & Coscarón, 1962), but such resemblance is clearly convergent. In the Oriento-Australasian Regions there are no known forms with pupal gills like those of *cervicornutum*-group.

Included taxa. *Simulium (Pomeroyellum) aureliani* Fain ; *S.(P.) blacklocki* de Meillon ; *S.(P.) cervicornutum* Pomeroy ; *S.(P.) leberrei* Grenier, Germain & Mouchet ; *S.(P.) palmeri* Pomeroy ; *S.(P.) pauliani* Grenier & Doucet ; *S.(P.) rotundum* Gibbins ; *S.(P.) unicornutum* Pomeroy ; *S.(P.) vangilsii* Wanson.

In addition the nomenclaturally unavailable form name *bertrandi* has been applied by Luna de Carvalho (1962) to a taxon of this group.

**kenyae-group.** ♂ hind basitarsus enormously enlarged, width about one-third of length ; styles normal ; ventral plate with well developed shoulders and excavate sides, very deep in profile (Text-fig. 122). Pupal gill with eight long filaments arising near base in regular pairs (Text-fig. 184). Cocoon with neck. Larval abdomen posterodorsally with very small semi-recumbent multifid setae (Text-fig. 225*d*) ; accessory sclerites absent. Larval postgenal cleft very large, much longer than postgenal bridge, with flattened-cordate or transversely ovate shape (Text-fig. 249) in which long axis is transverse.

This group is proposed for the single species *S.(P.) kenyae* which certainly belongs in the subgenus *Pomeroyellum* on its aggregate of characters, but which is so distinctive in several features that it cannot satisfactorily be placed in any of the other species-groups. The male differs from all other black-flies in the Ethiopian Region by having the hind basitarsus very greatly dilated (figured by Freeman & de Meillon, 1953 : 80), so that the length is only about three times the greatest breadth ; in other species where the male hind basitarsus is expanded the length is normally at least four times as long as the width. The cocoon in *kenyae* has a well developed neck, and thus differs from that of other species of *Pomeroyellum*, and the shape of the larval postgenal cleft in which the width is greater than the length is very unusual.

The female differs from typical species of *Pomeroyellum* by the bright golden scaling on the thorax and most of the abdomen, and by lacking the usual sub-basal dark band on the tibiae.

The male hypopygium, especially shape of the ventral plate, closely resembles that of the *cervicornutum*-group and of *S.(P.) mcmahoni* de Meillon in the *schoutedeni*-group, but the vestiture of the larval abdomen in the form of compound deeply multifid setae with the branches further bifurcated (see figure 8E in Garms & Post, 1967) is closely akin to that of the *alcocki*-group.

*S.(P.) kenyae* is a swift-water species occurring in rocky turbulent habitats to which the immature stages show clear adaptation in the necked cocoon (not found in other species of *Pomeroyellum*) and by the greater number of hooks in the posterior circlet of the larva (about 85 rows of 13–16 hooks instead of about 60–70 rows of 8–14 hooks as is usual in other species of the subgenus).

The pupal gill with its eight filaments branching in four regular pairs from very short common stems lying in the same plane (Text-fig. 184) is unique among Ethiopian Simuliidae, although this is a very common form of gill among the Palaearctic species of *Simulium*. In other Ethiopian species with eight filaments there is a different branching arrangement; they arise from a common stem, or if in pairs (*S.(P.) rodhaini* Fain) one pair is in a different plane from the others.

Included taxon. *Simulium (Pomeroyellum) kenyae* de Meillon.

#### Subgenus **MEILLONIELLUM** Rubzov

*Meilloniellum* Rubzov, 1962 : 1496. Type-species : *Simulium hirsutum* Pomeroy, 1922, by original designation.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane bare or haired. Katepisternum bare. Fore tarsus slender, fore basitarsus about 5.5–7 times as long as its greatest breadth. ♀ : cibarium unarmed. Tarsal claws with large basal tooth. Scutum without pattern. Abdomen thickly and evenly covered with pale scales. Seventh sternite developed. Gonapophyses simple bluntly rounded lobes. Paraprocts normal. Spermatheca without surface pattern or internal hairs. ♂ : scutum without pattern, with thick pale scales marginally. Genitalia with small styles much shorter than coxites, style abruptly contracted subapically and with attenuate tip, one apical spinule; coxite not produced beyond base of style; ventral plate not toothed, with very small subparallel basal arms, subrectangular with deep median apical emargination, broad in profile (Text-fig. 126); median sclerite strap-like; parameres long and narrow, with one long strong parameral hook. *Pupa* : Gill filamentous, 6, 8 or 11 filaments; gill a little shorter than pupal body. Abdominal onchotaxy normal, pair of small hooks ventrally on segment 4 in addition; segments 6 or 7–9 dorsally with spine-combs. Cocoon simple, without neck or median projection. *Larva* : Head and cephalic fans normal. Hypostomium with usual nine apical teeth, these sharp and median and corner teeth prominent; hypostomial setae 3–5 in each row, rows lying parallel to lateral margin of hypostomium. Head-spots negative, on cephalic apotome surrounded by dark pigmentation forming H-shaped mark. Postgenal cleft much longer than postgenal bridge, large and subcircular. Mandible normal, second comb-tooth smaller than first and subequal to third; two mandibular serrations without supernumeraries. Antenna long and slender, with four segments. Thoracic cuticle bare. Abdominal cuticle posterodorsally with minute simple spinous hairs. Abdominal shape normal, broadest in profile at sixth or seventh segment. Ventral papillae present but usually small,

blunt and inconspicuous. Accessory sclerites present but sometimes only minute weakly sclerotized trace. Rectal scales present. Rectal gills with secondary lobules, sometimes small and very few or one lobe simple. Posterior circlet usually with 70-80 rows of 8-15 hooks.

**Bionomy.** Eggs clustered, adhered to substrate. Larval and pupal stages non-phoretic ; attached to varied substrates but mainly trailing herbage in wide variety of stream and river habitats, including rapids and large sandy-bedded rivers ; immature stages recorded from unusual ecological habitats of lacustrine wave-action and brackish estuarine waters. Female occasionally anthropophilic, probably normally ornithophilic.

**Distribution.** Confined to, and widespread in, the Ethiopian Region (Map 4) excluding southern Arabia.

**Discussion.** Rubzov (1962) erected the genus *Meilloniellum* for the species placed by Freeman & de Meillon (1953) in their *hirsutum*-group, with *Simulium hirsutum* Pomeroy as type-species. The segregate is here accepted as valid with subgeneric status, but in a more restricted sense than that of Rubzov. The subgenus here defined contains only the small free-living forms previously placed in the *hirsutum*-group, and excludes all those Ethiopian *Simulium* in which the larval and pupal stages live in obligate phoresis with crabs or nymphal mayflies : the phoretic forms are best placed in separate subgenera for the reasons discussed under the names *Lewisellum* sgen. n. and *Phoretomyia* sgen. n.

I agree with Rubzov that *hirsutum* and its immediate allies are best placed in a genus-group segregate distinct from *Pomeroyellum*, but it must be admitted that it is difficult to formulate differential diagnoses that are completely adequate for distinguishing *Meilloniellum* from *Pomeroyellum* at all stages. The two subgenera are probably closely related, since they have in common the following characters : basal section of radius haired, large claw-tooth in female, similar female terminalia, scutum of both sexes without pattern, non-dilated fore tarsi, haired ventral plate, one main parameral hook in each parameral organ, short styles, simple slipper-shaped cocoon and same type of filamentous pupal gill, similar pupal abdominal armature, larvae with negative head pattern and similar mandibles.

The pupal stages of *Meilloniellum* and *Pomeroyellum* are subgenerically inseparable, but other stages show the following distinctions : ♀ abdomen thickly covered with silvery or silver-yellow scales in *Meilloniellum* (posterior part normally bare and shining in *Pomeroyellum* although a few species with complete thick vestiture) ; ♂ style abruptly contracted before the end, and terminal third bearing the spinule attenuated (never of this form in *Pomeroyellum*) ; ♂ ventral plate in *Meilloniellum* with broad deep median apical notch (without such emargination in *Pomeroyellum*) ; larval abdominal cuticle posterodorsally with minute simple setae in *Meilloniellum* (i.e. not with complex divided setae, flattened scales or bare as in *Pomeroyellum*).

From *Eusimulium*, to which there is undoubtedly a general relationship, *Meilloniellum* is distinguished by the negative larval head pattern, shape of the male styles, and to a lesser extent by the shape of the ventral plate. The characters separating the subgenus from *Lewisellum* and *Phoretomyia* are enumerated elsewhere in the

treatment of these subgenera ; from the Oriento-Australasian subgenera *Gomphostilbia* and *Morops* it is distinguished by almost all the characters separating these from *Pomeroyellum* already given.

One species of the subgenus, *Simulium* (*Meilloniellum*) *adersi* Pomeroy, is unique among all the more 'primitive', or at least less specialized, Ethiopian species of *Simulium* (those in subgenera *Eusimulium*, *Pomeroyellum* and *Meilloniellum*) in having the pleural membrane haired ; all other characters however confirm the position of *adersi* in *Meilloniellum*.

Attention should be drawn to the nature of the setae on the larval abdomen. For brevity, these have been described in the diagnosis and foregoing discussion as simple spinous setae but the actual shape is slightly fusiform or very narrowly lanceolate as the setae are slightly widened near the middle from which they taper to a point (well shown by Garms & Post, 1967, fig. 7L).

Included taxa. *Simulium* (*Meilloniellum*) *adersi* Pomeroy ; *S.*(*M.*) *hirsutum* Pomeroy ; *S.*(*M.*) *sexiens* de Meillon ; *S.*(*M.*) *urundiense* Fain.

### Subgenus *LEWISELLUM* sgen. n.

Type-species : *Simulium neavei* Roubaud, 1915.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane bare. Katepisternum bare. Fore tarsus not dilated, about 5.25-7 times as long as its greatest breadth. ♀ : cibarium unarmed. Tarsal claws with small or minute basal tooth, sometimes virtually simple. Scutum without pattern. Abdomen thickly covered with scales\*. Seventh sternite usually distinct. Gonapophyses simple bluntly rounded lobes. Paraprocts normal. Spermatheca without surface pattern or internal hairs. ♂ : scutum without pattern. Genitalia with small styles much shorter than coxites, style abruptly narrowed on about apical third and with one spinule ; coxite not produced beyond base of style ; ventral plate not toothed, with large rounded shoulders and median apical U-shaped notch (Text-fig. 105), basal arms very small and directed more or less forwards ; median sclerite a large broad elongate band, parallel-sided or slightly constricted medially ; paramere small tapering subtriangular, one long very strong outwardly directed parameral hook (Text-fig. 89). *Pupa* : Gill filamentous, eight long slender sinuous filaments arising near base and branching in 3+3+2 arrangement (Text-fig. 195) ; gill as long as or longer than pupal body. Abdomen with normal basic onchotaxy and in addition with a row, usually of four, of small hooklets each side dorsally on segment 2 and some supernumerary minute hairs dorsally or dorsolaterally on segments 1, 2, 5 and 6, also one or two supernumerary dorsal hairs on hooklet-bearing segments 3 and 4 ; ventrally segment 4 with pair of small hooklets (in addition to normal two pairs of ventral hooks on segments 5-7) ; terminal segments dorsally without definite spine-combs, or with trace of rudimentary combs on segments 7 and 8. Cocoon simple, without neck or median projection. *Larva* : Head atypically elongate and cephalic apotome unusually parallel-sided (Text-fig. 283), posterior corners of cephalic apotome evenly rounded ; cephalic fans normal. Hypostomium atypical in older and mature larvae, with subequal teeth numbering thirteen in apical row and with lateral margins less strongly convergent than normal (Text-fig. 268) ; hypostomial setae 4-7 in each row, rows lying parallel to lateral margins of hypostomium. Head-spots negative, on cephalic apotome delimited by darker pigmentation forming H-shaped mark (Text-fig. 283), apotome sometimes rather evenly pigmented and spots indefinite. Postgenal cleft small, quadrate, much shorter than postgenal bridge (Text-fig. 251). Mandible atypical, long and slightly tapering with outer edge less arched

\* See Appendix

than normal (Text-fig. 292), main apical tooth greatly enlarged, other apical teeth and comb-teeth reduced (Text-fig. 297); two mandibular serrations, proximal one sometimes reduced. Antenna long and slender, with four segments. Thoracic cuticle bare. Abdominal cuticle bare (except for some small colourless simple setae posterodorsally) and with striate, crazed, or platelet-like microsculpture. Abdomen with posterior enlarged part unusually attenuate (Text-fig. 284). Ventral papillae absent. Accessory sclerites absent. Rectal scales present (? exceptions). Rectal gills with secondary lobules. Posterior circlet with about 120-160 rows of 16-25 hooks.

**Bionomy.** [Oviposition habit unknown.] Larval stages (except first instar) and pupal stage phoretic, attached to riverine crabs of genus *Potamonautes* Macleay (Crustacea : Decapoda : Potamidae) living in small river and stream habitats in lowland and upland areas. Female mammalophilic, including anthropophilic.

**Distribution.** Endemic subgenus in Ethiopian Region occurring in Cameroon, Congo Basin, and eastern Africa from Ethiopia southwards to Malawi (Map 5). Unknown from West Africa.

**Discussion.** The most remarkable *Simulium* ecologically are the forms found in tropical Africa in which the larval and pupal stages live in a state of obligate phoresis with river-crabs, a unique biological association occurring in no other Simuliidae from any region. These forms comprise such a distinctive, morphologically homogeneous, and ecologically clearly defined segregate in *Simulium* s.l. that they are best treated as a subgenus on their own ranking taxonomically equivalent with other subgeneric segregates; the subgenus *Lewisellum* sgen. n. is therefore here erected for them, with *S.(L.) neavei* Roubaud as type-species. Hitherto this species, and the others associated with crabs, have been placed in the *hirsutum*-group (Freeman & de Meillon, 1953) of *Simulium*, or together with the phoretic forms on mayfly nymphs in the *neavei*-group of *Simulium* (Crosskey, 1960), or have been placed in the genus *Meilloniellum* by Rubzov (1962).

It is probable that the phyletic affinities of *Lewisellum* do, in fact, lie with *Simulium hirsutum* Pomeroy and its allies in the subgenus *Meilloniellum* Rubzov, since there is a close resemblance in the form of the ventral plate and styles of the male hypopygium between the two groups (such that it is improbable that the resemblances arose convergently). There is also a close concordance of other adult characters, male and female, and of pupal form between *Lewisellum* and *Meilloniellum* although the pupal abdomen in *Lewisellum* has a number of supernumerary hairs on the dorsum that are not represented in the latter subgenus. The adults of *Lewisellum* superficially differ much from those of *Meilloniellum* species by their large size (wing-length 2.6-3.6 mm., usually about 3 mm., in *Lewisellum*, and about 2-2.5 mm. in *Meilloniellum*) and by striking appearance through golden scaling on the scutum and thick golden or golden and bronze-brown scaling on the abdomen.

The larvae of *Lewisellum* species show a number of aberrant, or at least slightly atypical, characters that set them apart from those of all other subgenera: these include the reduction of the eye-spots, shape of the head and cephalic apotome, form of the mandible, form of the mature larval hypostomium, abdominal shape and cuticular surface pattern. Some of these are presumably adaptations for life on the

phoretic partner, although it is difficult to discern the significance of most of the departures from the morphological norm in Simuliidae. The hypostomium (Text-fig. 268), with a rather regular row of thirteen instead of the normal nine apical teeth, has a form unique among black-flies, but it is important to note that this form is not acquired until late on in larval development, for the early instar larvae have a normal type of hypostomium with prominent median and corner teeth and an apical row containing nine teeth altogether as in free-living forms; the mature larval 13-tooth row appears to be derived by an enlargement and forward migration during development of the paired blunt serrations that lie immediately behind each corner tooth in the normal hypostomium.

The larval abdominal cuticle in *Lewisellum* species shows a more definite microsculpture than in most Simuliidae and the nature of the cuticular thickening, whether irregularly striate, with close-set ovoid plaque-like thickenings, or with a crazed crack-like pattern, provides a taxonomic character for distinguishing species: the character has been illustrated by Grenier & Mouchet (1959) and Lewis (1961). It is not yet clear how valuable the existence of the microsculpture might prove as a diagnostic subgeneric character.

Mature larvae and the pupae of *Lewisellum* never occur, or at least have never been found, in a 'free-living' state attached to the normal types of substrate selected by *Simulium* larvae, such as on rock, stones, trailing roots and grasses, fish-traps and other objects in the watercourses, and it is clear that the phoretic association with crabs is an obligate one for maintenance of the life cycle. The egg-laying habits of the species of *Lewisellum* are still not known, but neither eggs nor first instar larvae have as yet been found on the crab partners; attachment to these probably occurs at or as soon as possible after the second instar. Nothing is known of the mechanism of crab location.

Most of the African river-crabs belong to *Potamonautes* Macleay and the immature stages of the species of *Lewisellum* are only known to be associated with this genus of crabs. The species of *Potamonautes* occur widely throughout Africa in both the warmer lowland and cooler upland rivers and streams, but crab and simuliid associations are known mainly from cool highland habitats in East Africa (possibly because these habitats have been more intensively studied than the lowland ones). The subgenus *Lewisellum* is best known from such mountain areas as western Kenya, Mount Elgon, Ruwenzori and Kigezi, and the Usambara Mountains, but it occurs in many lowland localities in the Congo Basin, and is almost certainly much more universally distributed in the equatorial belt of Africa than is apparent from the map of present known distribution (Map 5): nevertheless, most species of *Potamonautes* appear to have a wider distribution than the black-fly species that are associated with them. In East Africa nine out of the thirty-one species of river-crabs are known to act as carriers in phoretic associations with black-flies (Williams, 1968), but there is little or no evidence suggesting that a particular species of black-fly is associated with a particular crab species.

The subgenus *Lewisellum* appears to be absent from West Africa, since no crab-simuliid relationships have been discovered in Nigeria or anywhere further to the

west, and no adult Simuliidae assignable to the subgenus have been found in West Africa ; it is probable that this is a genuine fact of distribution, and not an artifact from inadequate knowledge. It is possible that the subgenus evolved in the Rift Valley region of eastern Africa with subsequent westward dispersal to the Congo Basin and Cameroon.

Included taxa. *Simulium (Lewisellum) goinyi* Lewis & Hanney ; *S.(L.) hightoni* Lewis ; *S.(L.) neavei* Roubaud ; *S.(L.) nyalalandicum* de Meillon ; *S.(L.) ovazzae* Grenier & Mouchet ; *S.(L.) woodi* de Meillon.

### Subgenus *PHORETOMYIA* sgen. n.

Type-species : *Simulium copleyi* Gibbins, 1941.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane bare. Katepisternum bare. Fore tarsus usually strongly dilated and with short dorsal hair crest, fore basitarsus 4-5 times as long as its greatest breadth (except *berneri* in which 6-7 times longer than broad). ♀ : cibarium unarmed. Tarsal claws with medium size to large basal tooth, rarely small and blunt. Scutum without pattern or with broad median longitudinal dark band flanked by paler lateral areas. Abdomen very thickly covered with pale yellow to golden scales on first two segments, other segments mainly with dark or scattered patches of pale scales, terminal segments sometimes shining and with sparse hairs only. Seventh sternite at least weakly developed. Gonapophyses simple bluntly rounded lobes. Paraprocts normal. Spermatheca without or with weak traces of polygonal pattern, without internal hairs. ♂ : scutum as in female. Genitalia with small styles shorter than coxites, style curved subconical and with one apical spinule ; coxite not produced beyond base of style ; ventral plate not toothed, large but longer than its width with rounded shoulders, very small forwardly directed basal arms, at least a trace of median apical emargination, and usually with a small median notch in the anterior margin between the basal arms (Text-fig. 106) ; median sclerite long and slender, parallel-sided, strap- or rod-like ; parameres narrow and irregular, with one long strong parameral hook (sometimes with small supernumerary hook at its base), or without definite hook but with a small slender irregular terminal process. *Pupa* : Gill with very slender thread-like filaments, numbering from 10-95, mainly arising individually near base, when filaments very numerous, gill assuming semicircular shape (Text-figs. 198 & 199) ; gill normally shorter than pupal body. Abdominal onchotaxy varied, sometimes with normal basic hook plan plus a pair of hooklets ventrally on segment 4, sometimes aberrant and some segments showing supernumerary hooks dorsally, or segments 5-8 girdled with supernumerary blunt hooklets ; terminal segments dorsally without spine-combs. Cocoon a simple pocket without neck or median projection, often shorter than normal and sometimes covering only the abdomen or abdomen and posterior third of thorax. *Larva* : Aberrant from typical *Simulium* in many characters. Head shape usually atypical, sides often strongly convex and cephalic apotome broadest near or slightly behind the middle and contracting thence towards hind margin of head (Text-fig. 286) ; cephalic fans either normal or aberrant, in latter case forming when open a short flat brush of almost straight or slightly sinuous rays curved only at the tips. Hypostomium atypical in older and mature larvae, of varied forms (Text-figs. 265-267) ; hypostomial setae 3-7 in each row, sometimes irregular, rows lying parallel to lateral margins of hypostomium. Head-spots indefinite, cephalic apotome lightly pigmented and usually with trace of paler negative spots, sometimes spots apparently darker than surrounding areas, occasionally head suffused with dark pigmentation on posterior half of cephalic apotome and on bulbous lateral areas. Postgenal cleft absent so that whole floor of head is sclerotized (Text-fig. 252), or at most represented by shallow inconspicuous usually subrectangular notch, postgenal bridge therefore virtually continuous to hind margin of cranium.

Mandible atypical, main apical tooth usually very large relative to other apical teeth, comb-teeth usually much reduced (Text-fig. 299) ; at most two small mandibular serrations, these usually reduced or obliterated. Antenna short or very short, with four segments or with only three segments because of loss of suture between the normal basal two. Thoracic cuticle bare or with small pale hairs. Abdominal cuticle bare or with covering of minute colourless hairs, sometimes microstriate at least posteriorly. Abdominal shape atypical, posterior cirlet in almost ventral position (Text-fig. 285), anal sclerite almost terminal and not dorsal, arms of anal sclerite unusually slender, last abdominal segment sometimes produced as a posterodorsal bulbous lobe almost overhanging the anal opening. Ventral papillae absent. Accessory sclerites absent. Rectal scales apparently absent. Rectal gills with numerous long finger-like secondary lobules. Posterior cirlet with about 90-100 rows of 14-23 hooks, usually about 94 rows of about 18 hooks.

Bionomy. [Oviposition habit unknown.] Larval stages (with probable exception of first instar) and pupal stage phoretic, attached to nymphal stages of fluvial mayflies (Ephemeroptera : Heptageniidae, Baetidae, Oligoneuriidae) living mainly in stony torrents\*. [Female biting preferences unknown.]

Distribution. Endemic subgenus confined to the Ethiopian Region, known from equatorial Africa from Ghana eastwards through Cameroon and northern Angola to Uganda, Kenya and Tanzania (Map 6) ; at present there is a large break in confirmed distribution in the Congo basin.

Discussion. The new subgenus *Phoretomyia* is here erected, with *Simulium copleyi* Gibbins as type-species, to include all the species of *Simulium* from tropical Africa that in their immature stages live in an obligatory phoretic relationship with nymphal mayflies. These forms are ecologically distinct from all other black-flies in the Ethiopian Region, and from almost all other world *Simulium* ; simuliid-mayfly relationships are unknown in the New World and in the Australasian Region, but have been recorded in the Oriental Region and one Palaearctic species (*Simulium ephemerophilum* Rubzov from Soviet Central Asia) of simuliid attaches to mayflies. The Ethiopian species with this habit differ not only biologically but also morphologically from other segregates of the *Simulium* fauna in Africa, and it is impossible to place them satisfactorily in any of the already named subgenera ; they are therefore here placed in the new subgenus on their own, and ranked as an equivalent taxon to the phoretic forms on crabs in the subgenus *Lewisellum* and to each of the free-living segregates of subgeneric status.

The species of *Phoretomyia* are fairly uniform as adults, but rather heterogeneous in the larval and pupal stages, which are strikingly aberrant compared with those of typical free-living *Simulium* ; the pupal abdomen often bears numerous additional hooks that are supernumerary to the normal basic onchotaxy found in *Simulium* pupae, the larval head is sometimes broadly bulbous with the cephalic apotome widest near the middle (recalling the condition of the head in the genus *Prosimulium* or in *Gymnopsais*), the cephalic fans may be curiously modified and the hypostomium, mandibles and abdominal shape of the larva all differ from those of typical *Simulium* ; in forms with additional pupal abdominal hooks there is a correlated reduction of size of the cocoon, that may only cover the pupal abdomen. Some of these departures from the norm for the genus *Simulium* are clearly adaptations to life on the

\* Also attached to river prawns, see Appendix

phoretic partner, particularly the shift of the posterior larval cirlet to an almost completely ventral (instead of terminal) position and the reduction of the cocoon and associated multiplication of securing hooks ; on the other hand it is difficult to see the significance of some of the structural modifications that occur in the larvae, for instance the extreme reduction of the antennae in *S.(P.) lumbwanum* de Meillon, the aberrant head fans in *S.(P.) copleyi* Gibbins, or the unique form of hypostomium in *S.(P.) bernerii* Freeman, although they are presumably related in some way to the demands of a larval life spent attached to motile mayflies.

The adults of *Phoretomyia* are moderately large (wing-length about 2.9–3.3 mm.) and are particularly striking and handsome among African *Simulium* because of the thick and even covering of rich yellow to deep golden scales on the first two abdominal segments (discounting the basal scale) that contrast very conspicuously with the remainder of the abdomen which is black (either with bronze-black scales and sparse black hairs, or with bronze-black scales intermixed with clumps of pale yellow to golden scales). In most species the fore tarsi are enlarged and flattened with a short dorsal hair crest (e.g. *Simulium copleyi* Gibbins, Text-fig. 81) and the fore basitarsus in these forms is usually only about 4.5 times as long as its greatest width ; this strongly dilated fore tarsus distinguishes most *Phoretomyia* from almost all other Ethiopian *Simulium* except the species of subgenus *Edwardsellum* such as *S.(E.) damnosum* Theobald (Text-fig. 82), in which the fore tarsus is similarly enlarged, but the resemblance between *Phoretomyia* and *Edwardsellum* in this character is certainly convergent.

The characters of the immature stages, being largely aberrant as compared to those of typical *Simulium* and apparently adaptive characters rapidly evolved for phoretic life, cannot safely be used for attempting to determine the phyletic affinities of the subgenus *Phoretomyia* ; only adult characters can be considered for this purpose. Of these the haired base to the radius, the lack of definite scutal pattern, the toothed claws of the female, the smoothly rounded gonapophyses of the female terminalia, the retention of a more or less definite seventh sternite in the female abdomen, the small simple male styles, the presence of only one long main parameral hook and of a haired lamellate ventral plate in the male hypopygium all indicate general affinity with the more primitive (or at least most generalized) subgenera of *Simulium* such as *Eusimulium*, *Pomeroyellum* and *Meilloniellum*, and particularly with *Meilloniellum*.

The Ethiopian species living in association with mayflies were, in fact, assigned by Rubzov (1962 : 1497) to his genus *Meilloniellum*, erected by him for all the species previously placed in the *hirsutum*-group of *Simulium* by Freeman & de Meillon (1953), and it is to *hirsutum* Pomeroy and its allies (here treated as the subgenus *Meilloniellum* in a more restricted sense than that of Rubzov) that the phoretic forms on mayflies appear most nearly related : this is suggested especially by the form of the male ventral plate, which is closely similar in *Meilloniellum* and *Phoretomyia*, and for instance almost identical in *S.(M.) hirsutum* Pomeroy and *S.(P.) lumbwanum* de Meillon. On balance of characters, excluding the difference of ecological habit and associated larval and pupal modifications, a better classification into subgenera

results if the phoretic forms on mayflies (like those on crabs) are separated as a discrete subgenus—despite the obvious resemblance in the form of the male hypopygium: the new resultant subgenus *Phoretomyia* here described is distinct from *Meilloniellum*, apart from the immature stages, on the large size and quite different abdominal vestiture, by the tapering subconical shape of the styles, and by the enlarged flattened tarsi occurring in the majority of forms. These same characters also distinguish the adults of *Phoretomyia* from those of the subgenus *Lewisellum* in which the immature stages live in phoretic association with crabs.

The constituent taxa in the subgenus *Phoretomyia*, despite the diversity of the immature stages, are considered to be monophyletic because of the clear homogeneity of the adult stage. But the widely differing larvae and pupae make it convenient to recognize three small species-groups within the subgenus; these are clearly natural groups, defined ecologically by phoretic association with particular genera of mayflies as well as by morphological differences.

The species-groups are keyed and defined below.

#### KEY TO THE SPECIES-GROUPS OF THE SUBGENUS *PHORETOMYIA*

##### IMMATURE STAGES

Note: in the following key the genus of mayflies to which attachment occurs is shown in brackets.

- 1 Larval hypostomium with a very large median tooth flanked by five blunt teeth on each side (Text-fig 267). Larval cuticle covered with colourless hairs. Cocoon normal, covering pupal thorax and abdomen. [Attached to *Elassoneuria*] **berneri-group** (p. 83)
- Larval hypostomium not of this form. Larval cuticle bare. Cocoon reduced, covering only pupal abdomen or abdomen and posterior part of thorax. [Attached to other mayfly genera] . . . . . 2
- 2 Larval cephalic fan in form of short flat brush, sides of larval head strongly convex and cephalic apotome broadest near middle (Text-fig. 286). Larval antenna conspicuous, almost as long as stem of cephalic fan. Pupal abdomen bare on segments 5–8 (except at most for two or three small spiny hooklets each side on 5). [Attached to *Afronurus*, *Baetis* and unidentified Baetidae] . . . . . **copleyi-group** (p. 84)
- Larval cephalic fan when open forming usual hemispherical brush, sides of larval head not convex and cephalic apotome broadest posteriorly. Larval antenna inconspicuous and colourless, only about half as long as stem of cephalic fan. Pupal abdomen girdled with numerous blunt hooks on segments 5–7 and with similar hooks laterally on segment 8 (Text-figs. 170 & 173). [Attached to *Afronurus*] **lumbwanum-group** (p. 83)

##### ADULTS

- 1 ♂ hypopygium without properly formed parameral hooks, these represented by an irregular rudimentary process on end of each paramere (except in *diceros*). Postnotum with patch of yellow or golden scales on each side (except in *diceros*) **copleyi-group** (p. 84)
- ♂ hypopygium with one long strong parameral hook on each side, sometimes with small supernumerary hook at base of main hook. Postnotum bare . . . . . 2
- 2 Scutum with black-brown scales on a broad median longitudinal area and with

- golden scales laterally. Fore tarsi dilated, the basitarsus about 4.5 times as long as its greatest breadth . . . . . **lumbwanum-group** (p. 83)
- Scutum with golden scales only. Fore tarsi narrow or enlarged, the basitarsus 4.5-7.0 times as long as its greatest breadth . . . . . **berneri-group** (p. 83)

**berneri-group.** Fore basitarsus narrow or enlarged, 4.5-7.0 times as long as its greatest width. Postnotum bare. ♂ hypopygium with one long strong parameral hook on each side, sometimes with additional small hook. Pupal gill with 38-95 filaments (Text-fig. 199). Pupal abdomen with normal *Simulium* onchotaxy. Cocoon complete, covering pupal thorax and abdomen. Larval head not noticeably convex, cephalic apotome broadest near hind margin or only slightly forward; cephalic fans when open forming usual hemispherical brush, the rays exceptionally slender and filter apparatus very inconspicuous. Larval antenna about as long as stem of cephalic fan, with four segments. Hypostomium of unique form (as Text-fig. 267). Mandible with main apical tooth very large basally, only one small mandibular serration and comb-teeth very reduced. Thoracic and abdominal cuticle covered with fine colourless hairs, these mostly slightly clubbed apically. Abdominal segmentation unusually well marked.

This small group contains two little known species that occur as larvae and pupae only on the large mature or almost mature nymphs of unidentified species of *Elassoneuria* Eaton (Ephemeroptera: Oligoneuriidae). To date, associations between *berneri*-group species and *Elassoneuria* mayflies have been recorded only from Ghana, Cameroon Republic, northern Angola, and western Uganda but the distribution is likely to be much more widespread than the existing records suggest, and probably other species of the group remain to be discovered. For some years only *S. berneri* Freeman was known to occur in phoretic relationship with *Elassoneuria*, but a second species (*S. kumboense*) has recently been described by Grenier *et al.* (1965a): in the original description *kumboense* was given the status of a subspecies of *berneri*, but Germain *et al.* (1966: 135, footnote) later suggested that *kumboense* and *berneri* are two distinct species. They are here provisionally treated as separate species, though undoubtedly extremely closely allied. Ecological aspects of the association between *S.(P.) kumboense* and *Elassoneuria* have recently been discussed by Germain & Grenier (1967).

Included taxa. *Simulium* (*Phoretomyia*) *berneri* Freeman; *S.(P.) kumboense* Grenier, Germain & Mouchet.

**lumbwanum-group.** Fore tarsus enlarged, basitarsus about 4.5 times as long as its greatest width. Postnotum bare. Scutum with pattern formed by broad median longitudinal band of black-brown or bronze scales with golden scales on either side. ♀ abdomen shining and bare except for sparse fine erect hairs on last few segments, thick scales confined to base and sides. ♂ hypopygium with one long strong hook in each parameral organ. Pupal gill with 25-41 filaments (Text-fig. 198). Pupal abdomen unique among *Simulium*, exceptional onchotaxy with a girdle of 22-24 blunt hooks around each segment from 5-7 and with from 4-7 similar irregular blunt hooks each side on segment 8 (Text-figs. 170 & 173) in addition to the normal row of four hooks each side dorsally on segments 3 and 4; also some supernumerary spinous hairs or minute hooklets dorsally on segments 2-4 (Text-fig. 170). Cocoon reduced, covering only pupal abdomen. Larval head not convex, cephalic apotome broadest near hind margin; cephalic fan when open forming hemispherical brush, the rays exceptionally slender and filter apparatus very difficult to see. Larval antenna colourless and reduced (difficult to see), only about half as long as stem of cephalic fan, first two segments lacking suture between. Hypostomium with nine apical teeth (as in normal free-living *Simulium*) but median and corner teeth

exceptionally long (Text-fig. 265). Larval mandible with two serrations, comb-teeth few but long and first three comb-teeth blunt apically (Text-figs. 293, 298). Larval cuticle bare. End of abdomen bulbously produced to overhang anus and anal sclerite.

This group contains only the single species *lumbwanum* de Meillon, but it is possible, as Freeman & de Meillon (1953 : 129) have pointed out, that the species known under this name may be a compound of two species (or possibly more). The characters of *lumbwanum* taken together, but in particular the extraordinary pupal abdominal onchotaxy with its girdles of irregularly arranged hooks around the fifth to eighth segments (not found in the same form in any other *Simulium*), make it impossible to assign the species satisfactorily to either the *berneri*-group or the *copleyi*-group and a monospecific group on its own is necessary for it. It resembles the *berneri*-group in having a well formed parameral hook each side in the male hypopygium and in the larval cephalic fans, but resembles the *copleyi*-group more closely in having the larval cuticle bare (although a few specimens, apparently of *lumbwanum*, have been seen in which the posterodorsal part of the cuticle shows a few colourless papilliform prominences).

The larval cephalic fans of *lumbwanum* form when open a curved brush similar in shape to that of all typical forms of *Simulium*, but the rays composing the fan are exceptionally slender and appear to lack a filter apparatus ; this, although in fact present, is so delicate that it is difficult to make out its structure even with phase-contrast examination. Exactly similar long very narrow rays with almost invisible filter apparatus occur also in the cephalic fans of the *berneri*-group, and the two groups together therefore have a very different type of feeding organ from that occurring in the *copleyi*-group (as described under this group heading below). The functional significance of this difference is not yet clear.

The *lumbwanum*-group is known mainly from Kenya, but occurs around Mount Elgon in eastern Uganda. Corbet (1960a) recorded *lumbwanum* from Ripon Falls on the Victoria Nile in Uganda and material on which this record is based is in the British Museum (the identity is confirmed) : it is now probable, however, that insecticidal operations in the Victoria Nile have eliminated *lumbwanum* from this site. A single pupa of the species (in B.M. collection) is known from the Victoria Falls on the Zambesi River. The distribution, as at present known, does not appear to overlap with that of the *berneri*-group which has a more westerly distribution, and is associated with *Elassoneuria* mayflies : the *lumbwanum*-group is only known to be associated phoretically with mayflies of the genus *Afronurus* Lestage (Ephemeroptera : Heptageniidae). At least two species of *Afronurus* (*A. ugandanus* Kimmins and *A. peringueyi* (Esben-Petersen)) act as carriers of immature *lumbwanum*, but there are probably others since many nymphs of *Afronurus* involved in the associations cannot be identified to species with certainty.

Included taxon. *Simulium* (*Phoretomyia*) *lumbwanum* de Meillon ; possibly also unrecognized semi-sibling species confused under this name.

**copleyi-group.** Fore tarsus enlarged (except *diceros*) and basitarsus 4-5 times as long as its greatest width, with dorsal hair crest (Text-fig. 81). Postnotum sometimes with patch of pale yellow to golden scales on each side. Scutum evenly covered with golden scales. Abdomen

with thick pale yellow or golden scaling on first two segments, and some pale scales laterally and intermixed dorsally with bronze-black scaling, terminal segments dorsally with sparse black hairs and semi-shining. ♂ hypopygium without properly formed parameral hooks (except *diceros*), these represented by small irregular process on end of each paramere. Pupal gill with 10-40 filaments, most often 17 (Text-fig. 197). Pupal abdomen with a normal basic onchotaxy supplemented by some supernumerary hooklets as follows : two hooklets each side ventrally on segment 4 (Text-fig. 172), a row of four or seven minute spinous hooklets each side dorsally on segments 3 and 4 (so that there are seven hooks each side on these segments in place of the normal four, Text-fig. 169), sometimes also two or three spinous hooklets each side latero-dorsally on segment 5. Cocoon reduced, covering only pupal abdomen or at most posterior part of thorax also. Larval head aberrant, sides bulbous and strongly convex, cephalic apotome widest near middle and contracting towards hind margin (Text-fig. 286) ; cephalic fan when open forming short flat brush, rays broad for most of their length then abruptly narrowed and slender at curved tips. Larval antenna conspicuous, slightly shorter than stem of cephalic fan, three-segmented through obliteration of first suture or four-segmented. Hypostomium with apical row of thirteen teeth, all or mostly rather blunt or rounded, formed from usual nine with outer two serrations on each side enlarged and produced forwards (as in Text-fig. 266 or with teeth shorter and blunter than this.) Larval mandible with main apical tooth very large and other apical teeth short and blunt, without mandibular serrations (though inner edge of mandible irregularly formed), comb-teeth very small or exceptionally minute (Text-fig. 299). Larval cuticle bare. Apex of abdomen as in Text-fig. 285.

The *copleyi*-group includes species in which the larval head has the most aberrant form found in any African Simuliidae, not only in the convexity and Prosimuliine-like shape of the cephalic apotome but in the form of the cephalic fans ; these, instead of the normal curved basket-like feeding brushes found in the vast majority of black-flies, have when open a flat subtriangular fan shape. The rays composing this flat fan, instead of being sickle-shaped, are mainly straight or slightly sinuous and relatively broad on most of their length, tapering abruptly to a fine curved tip on about the apical sixth ; the fine filter apparatus is very difficult to see and is confined to the slender tips of the rays only. At present it is uncertain what adaptive function is subserved by this exceptional modification to the normal mouth-brush, which is made the more puzzling by the fact that *S.(P.) lumbwanum*—which occurs in an apparently similar phoretic environment attached to the same genus of mayflies—has the usual form of hemispherical brush.

The *copleyi*-group species live in association with species of *Afronurus* Lestage (Heptageniidae) and *Baetis* Leach (Baetidae), and have also been found attached to nymphs of generically unidentifiable Baetids. It is not known how many and which species of mayflies are involved in phoretic associations with the group because of the difficulties of identification of African mayfly nymphs to the specific level, but in the genus *Afronurus* at least the species *A. negi* Corbet is concerned (Corbet, 1960b : 71) and almost certainly several others. The distribution of the *copleyi*-group appears to be centred mainly in East Africa and eastern Congo, but a species (*rickenbachi*) has recently been described from the Kumbo area of West Cameroon (Germain *et al.* 1966).

The poorly known species *S. diceros* Freeman & de Meillon is assigned here to the *copleyi*-group, to which it fits on its pupal characters and choice of phoretic partner ; but it should be emphasized that the slender fore tarsus, well formed parameral hook,

and bare postnotum of *diceros*, and apparently some of the larval characters (not seen, and as judged from the larval description given by Marlier, 1950 : 138), differ from those of *copleyi*, and the assignment to the group is tentative. Marlier's (1950) description under the name *S. neavei* was due to misidentification, and the name *diceros* should have been appended by Freeman & de Meillon (1953 : 123) with the suffix 'sp. nov.' and not 'nom. nov.'. *S. diceros* on adult characters would run to *berneri*-group in the foregoing key to species-groups.

Included taxa. *Simulium (Phoretomyia) copleyi* Gibbins ; *S.(P.) diceros* Freeman & de Meillon ; *S.(P.) marlieri* Grenier ; *S.(P.) rickenbachi* Germain, Grenier & Mouchet.

### Subgenus *XENOSIMULIUM* sgen. n.

Type-species: *Simulium imeriniae* Roubaud, 1905.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane bare or haired. Katepisternum bare. Fore tarsus slender, fore basitarsus 6.75–8 times as long as its greatest breadth. ♀ : cibarium unarmed. Tarsal claws with very small or minute pointed basal tooth. Scutum without conspicuous pattern, but with either three very fine longitudinal lines (seen from in front much as in *Wilhelmia*, Text-fig. 72), or with three broad dark-scaled vittae separated by pale-scaled areas. Abdomen with pale to coppery or blackish scales, evenly distributed or thinner on terminal segments so that these are semi-shining. Seventh sternite sclerotized, moderately well developed. Gonapophyses large and attenuate, pointed apices strongly haired and directed towards each other (Text-fig. 161). Paraprocts enlarged and slightly or distinctly produced downwards. Spermatheca with polygonal surface pattern, without internal hairs. ♂ : scutum [where known] similar to ♀. Genitalia with small tapering or slightly truncate styles that are subequal in length to or shorter than coxites ; style with one apical spinule ; coxites not produced beyond base of style ; ventral plate transverse with subparallel basal arms, not toothed ; median sclerite very large and broad, widening and bifurcate apically ; parameres elongate, parameral hooks numerous and varied in size. *Pupa* : Gill much shorter than pupal body, with 6–19 slightly stiff filaments not noticeably tapering and without sharp black tips. Abdominal onchotaxy normal, no supernumerary hooklets and all terminal abdominal segments without spine-combs dorsally. Cocoon with well developed neck. *Larva* : Head and cephalic fans normal. Hypostomium with usual nine apical teeth, but these very reduced and median and corner teeth hardly at all prominent ; hypostomial setae 7–10 in each row, sides of hypostomium very wide posteriorly and strongly divergent from hypostomial rows. Head-spots positive, sometimes partially concealed in extensive dark pigmentation. Postgenal cleft of medium size, pentagonal, slightly shorter than or subequal in length to postgenal bridge, sometimes narrow lightly sclerotized line extending forwards from cleft to hypostomium. Mandible with exceptionally large, apically prominent and strongly curved primary brush (Text-fig. 296), first three comb-teeth very large and longer than the unusually small apical teeth ; mandibular serrations usually two, sometimes one supernumerary serration or mandibular margin irregularly jagged. Antenna long and slender, secondarily annulated and appearing to have 6–8 segments. Thoracic cuticle bare. Abdominal shape normal, in profile gradually widening to last segment then abruptly contracting to circllet. Abdominal cuticle bare. Ventral papillae absent. Accessory sclerites absent. Rectal scales present or (apparently) sometimes absent. Rectal gills simple, without secondary lobules. Posterior circllet with about 180–250 rows of about 24–30 hooks.

Bionomy. [Oviposition habit unknown.] Larval and pupal stages non-phoretic ;

attached mainly to stones and rock surfaces in clear swift cascading streams. Female mammalophilic, including anthropophilic.

**Distribution.** Confined to the Malagasy Region, where widespread in Madagascar (Map 7) and known also from Comoro Islands.

**Discussion.** Grenier & Grjébine (1958 : 986), when describing *Simulium ambositrae* from Madagascar, pointed out that ' Cette espèce, comme *S. neireti* Roubaud et *S. imerinae* Roubaud, fait partie du groupe *dentulosum* (Division B, groupe VI, de Freeman et de De Meillon) dans lequel les espèces malgaches *imerinae*, *iphias*, *ambositrae* paraissent constituer un sous-groupe homogène'; in the present work it is considered that this homogeneous group, endemic in the Malagasy Region, is best ranked as a separate subgenus near to, but distinct from, the subgenus *Anasolen* (i.e. the *dentulosum*-group in the restricted sense). The name *Xenosimulium* is here proposed for the subgenus, and *Simulium imerinae* Roubaud (since it is the species best known in all stages and both sexes) is designated as type-species.

*Xenosimulium* sgen. n. is the only subgeneric segregate of *Simulium* s.l. that is confined to the Malagasy Region, where it forms the main component of the Simuliid fauna in Madagascar. It differs from all *Simulium* found in the Ethiopian Region by the unusual form of the enlarged, pointed and inwardly-directed female gonapophyses (Text-fig. 161) and by the secondarily annulated larval antenna, which appears to have seven or eight segments instead of the normal four (Text-fig. 290). The larvae are also remarkable because of the very prominent and enlarged almost semi-circular form of the primary brush of the mandible (Text-fig. 296) which makes them almost unique among Simuliid larvae from the African area as a whole, although a smaller but somewhat similar development of the primary brush occurs in the larvae of *S. (Freemanellum) debegene* de Meillon from the African mainland; the reduction of the apical teeth and relative enlargement of the comb-teeth of the larval mandible is also a striking feature (Text-fig. 302). The larval rectal gills consist of three simple undivided lobes, without the numerous finger-like secondary lobules that are normally found in the larvae of cascade-inhabiting forms, and this character among others already mentioned distinguishes larvae of *Xenosimulium* from those of *Freemanellum*, *Anasolen*, and *Metomphalus* that have superficially similar larvae with the same body shape and lack of ventral papillae. The pupal thorax in *Xenosimulium* species is unusual in having small very sharp spinous tubercles in place of the normal flattened disc or platelet-like tubercles that are normally found on the thoracic dorsum in the majority of *Simulium* s.l. species.

*Xenosimulium* has the most characters in common with *Anasolen* and *Freemanellum* from the Ethiopian mainland, although there is a marked concordance of characters with the Neotropical subgenus *Grenierella* Vargas & Diaz Najera. It is most likely that *Xenosimulium* is closely related to *Anasolen* and *Freemanellum*, especially the latter, and that the group derives from forms that reached Madagascar from Africa: there is no evidence to suggest an Oriental origin, and *Xenosimulium* shows no affinity with any segregate in the Oriento-Australasian Regions (or with the Holarctic fauna).

Aside from the female genital, larval antennal and mandibular, and larval rectal

gill characters cited above, *Xenosimulium* differs from *Freemanellum* by having the katepisternum bare, the male styles short, the female abdomen with a moderately well developed seventh sternite, and the pupal gill with more than four filaments ; from *Anasolen* it differs by the presence of the female seventh sternite, the absence of sharp black tips to the pupal gill filaments, by the longer and much less pigmented larval antenna and by the bare larval abdominal cuticle (in *Anasolen* larvae there are at least a few minute simple setae posterodorsally on the abdomen). The characters shared in common with *Freemanellum* and *Anasolen* are enumerated in the discussion relating to the latter subgenus.

In the South American *Simulium* fauna the group most nearly resembling Madagascan *Xenosimulium* appears to be *Grenierella* Vargas & Diaz Najera, at least to judge from Wygodzinsky's (1949) excellent figures for the type-species, *Simulium* (*Grenierella*) *lahillei* Paterson & Shannon from Argentina, and from adult and pupal pelt material of *lahillei* in the British Museum collection ; but the significance of the resemblances is uncertain. Nevertheless, to facilitate comparison of the fauna of the African area with the Neotropical fauna it will be useful to indicate the similarities and differences between *Xenosimulium* and *Grenierella* :—

Shared characters : Basal section of radius haired ; katepisternum bare ; fore tarsus slender ; cibarium unarmed or almost so ; very small female claw-tooth ; similar scutum ; paraprocts produced downwards ; one style spinule ; haired ventral plate with transverse shape and very similar profile ; shoe-shaped cocoon ; stiff pupal gill filaments ; segments 6–9 of pupal abdomen without spine-combs dorsally ; same larval body shape and bare cuticle ; rows of hypostomial setae diverging posteriorly from lateral margins of hypostomium, hypostomial teeth short.

Differential characters : Female gonapophyses long pointed and directed inwards and male style not longer than coxite in *Xenosimulium* (gonapophyses not of this shape and male style longer than coxite in *Grenierella*) ; larval postgenal cleft at most subequal in length to postgenal bridge in *Xenosimulium* (much longer than postgenal bridge in *Grenierella*) ; larval antenna long and pale, with secondary annulations in *Xenosimulium* (short, pigmented, without secondary annulations in *Grenierella*) ; rectal gills simple in *Xenosimulium* (compound with very numerous slender secondary lobules in *Grenierella*).

Included taxa. *Simulium* (*Xenosimulium*) *ambositrae* Grenier & Grjébine ; *S.(X.) imerinae* Roubaud ; *S.(X.) iphias* de Meillon ; *S.(X.) neireti* Roubaud.

### Subgenus *ANASOLEN* Enderlein

*Anasolen* Enderlein, 1930 : 94. Type-species : *Anasolen adolffriedericianus* Enderlein, 1930 [= *Simulium dentulosum* Roubaud, 1915], by original designation.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane haired or sometimes bare. Katepisternum bare. Fore tarsus slender or slightly dilated, fore basitarsus 6–8 times as long as its greatest breadth. ♀ : cibarium unarmed. Tarsal claws with very small or minute tooth, sometimes almost simple. Scutum dull, without definite pattern. Abdomen evenly covered with pale or coppery scales, not shining. Seventh sternite undeveloped or at most trace of rudimentary sclerotization. Gonapophyses small pointed-subtriangular (Text-fig. 158), tips directed slightly towards each other, sometimes slightly curled. Paraprocts normal. Spermatheca with polygonal surface pattern, without internal hairs. ♂ : scutum without conspicuous

pattern. Genitalia with small truncate styles shorter than coxites, style with one apical spinule ; coxite not produced beyond base of style ; ventral plate transverse or subcordate with short subparallel or slightly divergent basal arms, plate not toothed and with haired apex, usually only slightly curved in profile ; median sclerite rod-like or short and broad with dilated and sometimes cleft apex ; parameres narrow and elongate, parameral hooks very numerous. *Pupa* : Gill with from 8 to 19 rather short stiff filaments variously branching, filaments of even thickness along their length or only slightly tapering, each filament with sharp pointed blackened tip ; gill much shorter than pupal body. Abdominal onchotaxy normal, no supernumerary hooks and all terminal segments without spine-combs dorsally. Cocoon with well developed neck. *Larva* : Head and cephalic fans normal. Hypostomium with usual nine apical teeth, teeth short and blunt, median and corner teeth only slightly prominent ; hypostomial setae exceptionally numerous, 8–29 in each row, when more than about ten or twelve setae present on each side the row is irregularly doubled or tripled and with several of the setae haphazardly clustered, general line of the rows widely diverging posteriorly from lateral margins of hypostomium. Head-spots positive, usually merged into extensive dark pigmentation of head. Postgenal cleft small, shorter than postgenal bridge, in form of subquadrate notch which is often slightly pointed anteromedially or produced so that anterior part of cleft is subtriangular. Mandible normal, comb-teeth large and usually regularly increasing in length from first to third, second comb-tooth sometimes shorter than those on either side, two serrations. Antenna of medium length, subequal to or slightly longer than stem of cephalic fan, pigmented, with four segments. Thoracic cuticle bare. Abdominal shape normal, gradually expanding to widest at seventh or eighth segment then abruptly contracting to circling. Abdominal cuticle appearing bare but with sparse minute simple setae (very inconspicuous) posterodorsally. Ventral papillae absent. Accessory sclerites absent or very faint trace present. Rectal scales present or (apparently) sometimes absent. Rectal gills with secondary lobules. Posterior circling with about 200–250 rows of 24–45 hooks.

*Bionomy.* Eggs clustered, adhered to substrate. Larval and pupal stages non-phoretic ; torrenticolous, immature stages attached to smooth rock-surfaces, stones, trailing tree-rootlets and other vegetation in very fast cascades, mainly in mountain streams and up to exceptionally high altitudes (known almost to 15,000 feet a.s.l.). Female occasionally anthropophilic (habits little known, probably normally ornithophilic but some non-biting forms with atrophied mouthparts occur).

*Distribution.* Confined to, and widespread in, the Ethiopian Region including southern Arabia (Map 7). Apparently absent from most of the Congo Basin and distribution sporadic in West Africa.

*Discussion.* This small homogeneous subgenus, especially distinctive in the pupal stage because of the pointed blackened tips to the gill filaments, contains large species (with larvae up to 13 mm. in length) with a striking ecological preference for the fastest cascading waters, often—although by no means invariably—in high mountainous locales. The segregate is especially characteristic of dashing high-altitude streams on the major mountain massifs of eastern Africa such as Mt. Kenya, Mt. Elgon and Ruwenzori, where *Anasolen* is the dominant (and often the only) subgenus of *Simulium* occurring above eight or nine thousand feet. Some forms occur at truly montane levels not far below the level of permanent snow ; on Ruwenzori *Anasolen* species are known to exist up to 13,100 feet and on Mount Kenya up to 14,700 feet, the highest known locality for Simuliidae on the African

Continent. In southern Africa and in West Africa, where land levels in general are lower than in East Africa and Ethiopia, *Anasolen* species occur at much lower altitudes of 2,500–5,000 feet, but with the same ecological restriction to cascade conditions. As with certain species of the subgenus *Metomphalus*, the smooth submerged rock surfaces under the cascading water often appear black from the enormous numbers in which *Anasolen* larvae and pupae thrive there.

The subgenus *Anasolen*, though rather clearly related to *Freemanellum* sgen. n. (also from the Ethiopian Region) and to *Xenosimulium* sgen. n. (from the Malagasy Region) is an isolated segregate of *Simulium* s.l. showing no evidence of close affinity with any subgeneric segregate in the Holarctic, Oriental or Australasian Regions. Outside of the African area the relationships appear to lie most closely with the subgenus *Grenierella* Vargas & Diaz Najera from South America, or at least with the type-species of this subgenus, *S.(G.) lahillei* Paterson & Shannon : in the absence of a complete revision of the segregates of Neotropical *Simulium* it is difficult to make a satisfactory comparison, but it is here considered that *Grenierella* can tentatively be accepted as a valid subgenus (Stone, 1963, places *Grenierella* as a synonym of *Chirostilbia* Enderlein but there seems as yet insufficient evidence for this) having many characters in common with, and probably phyletically close to, African *Anasolen*. The larval and pupal stages of *Grenierella*, judging from the excellent figures of *lahillei* given by Wygodzinsky (1949), do not appear to differ subgenerically from those of *Anasolen*, and have for instance the following characters conforming with those of the latter group : similar larval body shape with extremely numerous hooklet rows in the circlets, no ventral papillae, similar hypostomium, hypostomial setae, antennae and mandibles, and similar rectal gills, cocoon with long very well formed neck, similar form of stiff gill branches with pointed tips, similar lack of spine-combs dorsally on the pupal abdominal segments. The adults of *Grenierella* and *Anasolen* also conform in many characters (haired base to radius, slender fore tarsus, bare katapisternum, haired ventral plate, minute claw-tooth in female, unarmed or almost unarmed cibarium) but differ as follows : pleural membrane bare in *Grenierella* (usually but not invariably haired in *Anasolen*), male styles longer than coxites in *Grenierella*, scutum of female with definite pattern, the paraprocts enlarged and the gonapophyses somewhat rounded in *Grenierella*.

There are also some resemblances between *Anasolen* and certain other Neotropical segregates in particular characters : the pointed subtriangular form of the female gonapophyses is not unlike that found in subgenus *Notolepria* Enderlein and the larval postgenal cleft and the black-tipped pupal gill filaments resemble to some extent those of certain species of the New World subgenus *Hearlea* Vargas, Martinez Palacios & Diaz Najera, but both *Notolepria* and *Hearlea* have the basal section of the radius bare and differ by so many other major characters that it is unlikely that there is close phyletic relationship between these subgenera and *Anasolen*.

Within the African area there is little doubt that *Anasolen* is closely related to the subgenera *Freemanellum* and *Xenosimulium*, the three subgenera apparently forming a natural monophyletic group. In common they share the following characters : basal section of radius haired, scutum without strong pattern, cibarium unarmed,

fore tarsi slender, numerous parameral hooks, haired ventral plate, frons of female pollinose, female abdomen with more or less even scale covering, pupal gill filamentous but filaments usually rather stiff, pupal abdomen without dorsal spine-combs on terminal segments, cocoon with well formed neck, larval head with positive head-spots and hypostomial setae divergent posteriorly from margins of hypostomium, larval cuticle bare or at most with sparse minute setae posterodorsally, similar larval abdominal shape and no ventral papillae. The differences from *Freemanellum* and *Xenosimulium* are indicated in the discussion sections for these subgenera (q.v.).

The subgenus *Anasolen*, which is so strikingly orophilic, perhaps originated in eastern Africa in the mountain-building Pliocene period, thence possibly dispersing from an original East African locus into southern and West Africa and through Ethiopia via the Pliocene land-bridge into southern Arabia (where the type-species, *S. dentulosum*, is known to occur : see Crosskey, 1967b : 5). At least such hypothesis would account for the known pattern of distribution for the subgenus (Map 7). On the other hand, the existence of *Anasolen*-like forms in South America (i.e. subgenus *Grenierella*) might, assuming that the resemblance is due to recent monophyly and not to convergence through occupation of a similar ecological niche, imply quite another origin for the group.

Some forms of *Anasolen* that occur on Mt. Kenya and on Ruwenzori from about 10,000 feet above sea-level to the highest glacier-melt streams at about 13,000–14,500 feet (the very highest altitudes at which Simuliidae occur in Africa) are remarkable for structural modifications to the female head and mouthparts that occur in no other Ethiopian *Simulium* : McCrae (personal communication) has found that the females are microcephalic and that the mouthparts lack well developed apical teeth for biting, the latter feature suggesting that they cannot bite and are presumably therefore autogenous. The head of the microcephalic forms, both anteriorly and posteriorly (for instance in shape of the occipital foramen, postgenal lobes and extent of the postgenal membrane), does not differ noticeably from that of normal forms except in its reduced size.

The pupal gill in *Anasolen* species shows all numbers of filaments from 8 to 19, except for 13—which number of gill-filaments has not been found in any pupa despite the occasional variability that sometimes occurs (McCrae, personal communication).

There is a close uniformity in the species of *Anasolen* and no separate species-groups are recognized within the subgenus.

Included taxa. *Simulium* (*Anasolen*) *bisnovem* Gibbins ; *S.(A.) dentulosum* Roubaud ; *S.(A.) kauntzeum* Gibbins ; *S.(A.) masabae* Gibbins ; *S.(A.) ngabogei* Fain ; *S.(A.) nili* Gibbins ; *S.(A.) octospicæ* Gibbins ; *S.(A.) rhodesiense* de Meillon ; *S.(A.) shoae* Grenier & Ovazza ; *S.(A.) voltae* Grenier, Ovazza & Valade.

[Note : *Simulium* (*Anasolen*) *nili* Gibbins was only known with certainty from the type-locality of the Victoria Nile near Jinja, Uganda, and appears to have been incidentally eradicated by insecticidal control operations on the Victoria Nile directed against *Simulium* (*Edwardsellum*) *damnosum* Theobald.]

Subgenus **FREEMANELLUM** sgen. n.

Type-species: *Simulium berghei* Fain, 1949.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane haired (apparently sometimes bare in ♀). Katepisternum haired. Fore tarsus slender, fore basitarsus 6-7 times as long as its greatest breadth. ♀ : cibarium unarmed. Tarsal claws with large basal tooth. Scutum rich reddish brown without pattern except for trace of three fine longitudinal lines. Abdomen thinly covered with pale or coppery scales, not shining. Seventh sternite undeveloped. Gonapophyses slightly or distinctly produced tongue-like, tips rounded, directed rather downwards. Paraprocts slightly, or large and very strongly, produced ventrally (Text-fig. 163). Spermatheca without or with weak traces of polygonal pattern, without internal hairs. ♂ : scutum as in female. Genitalia with long slender curved styles as long as or longer than coxites, style with one apical spinule ; coxite not produced beyond base of style but sometimes with inner spinous process ; ventral plate of complex shape, not toothed, body of plate very strongly angled and apex strongly haired, longer than wide, the basal arms parallel or slightly divergent ; plate with a definite lobe developed between bases of basal arms ; median sclerite large, clove-shaped or broadly dilated and slightly bifurcate apically ; parameres narrow elongate, parallel-sided or contracting apically, with numerous subequal parameral hooks. *Pupa* : Gill much shorter than pupal body, with four rather strong filaments arising near base, filaments sometimes swollen basally or with minute pointed blackened tips. Abdominal onchotaxy normal, no supernumerary hooks on segment 4 ventrally and terminal segments all without spine-combs dorsally. Cocoon with well formed neck, often much produced anteroventrally. *Larva* : Head and cephalic fans normal. Hypostomium with usual nine apical teeth but these extremely blunt and sunken (Text-fig. 276) ; hypostomial setae 8-10 in each row, rows widely divergent posteriorly from lateral margins of hypostomium, sides of hypostomium outside the setae very wide. Head-spots positive, often merged into extensive dark pigmentation on cephalic apotome. Postgenal cleft large, much longer than postgenal bridge, shape elongate-ovate in species known (Text-fig. 254). Mandible with very large primary brush extending well beyond apex (Text-fig. 295), comb-teeth very large and longer than the rather reduced main apical tooth ; comb-teeth regularly enlarging from first to third ; mandibular serrations normally two, inner margin of mandible sometimes a little irregular. Antenna long and slender, pale, with four segments. Thoracic cuticle bare. Abdominal shape normal, gradually expanding and widest at seventh or eighth segment. Abdominal cuticle bare. Ventral papillae absent. Accessory sclerites absent. Rectal scales apparently absent. Rectal gills with secondary lobules. Posterior circlet with about 180-300 rows of 25-40 hooks.

Bionomy. [Oviposition habit unknown.] Larval and pupal stages non-phoretic; attached to rock surfaces and trailing rootlets in waterfalls or cascades, usually at high altitude in hilly or mountainous areas. [Female biting preferences unknown, probably ornithophilic.]

Distribution. An endemic Ethiopian subgenus known from eastern and southern Africa with a distribution from north-eastern Congo and Uganda to the Cape (Map 8)\*. One species recorded also from Guinea. Not known from Madagascar, where the related subgenus *Xenosimulium* sgen. n. occurs.

Discussion. The new subgenus *Freemanellum* is here proposed for a small group of species that have hitherto been placed in the *dentulosum*-group of *Simulium* by Freeman & de Meillon (1953) or in the genus *Anasolen* (of which *Simulium dentulosum* Roubaud is type-species) by Rubzov (1962) ; these species form a natural group of orophilic cascade-inhabiting forms having several morphological characters and

\* Also in Nigeria and Liberia, see Appendix

ecological preferences in common with *dentulosum* and its allies (comprising the subgenus *Anasolen* in the present treatment) but differing from these and other *Simulium* by several characters that make their recognition as a separate subgenus desirable for a balanced classification.

The most notable character of the subgenus *Freemanellum* is the presence of conspicuous hairing on either side of the katepisternal region of the adult thorax ; in all other subgenera of Ethiopian *Simulium*, and in most other world *Simulium*, the katepisternum is bare. Apart from the occasional presence of katepisternal scaling in *aureum*-group and *latipes*-group species of *Eusimulium*, the only other subgenera in which the katepisternum is haired are *Gomphostilbia* from the Oriental Region and Japan, and *Morops* from New Guinea and Australia, but both of these subgenera belong clearly among the more primitive forms of *Simulium* near to *Eusimulium* and have no close phyletic relationship with *Freemanellum*. It may be noted, though, that *Morops* and *Freemanellum* are the only two subgenera among world *Simulium* in which *both* the katepisternum and the pleural membrane are haired (except for occasional female specimens of *Freemanellum* in which the pleural membrane appears to be naturally devoid of hair).

In the Ethiopian fauna *Freemanellum* is most nearly related to the subgenus *Anasolen*, from which it differs (apart from the katepisternal character already mentioned) by large claw-teeth and at least slightly downwardly-produced paraprocts in the female, by the long narrow styles in the male, by the pupal gill always with four filaments, and by the larger more produced primary brush and reduced main apical tooth of the larval mandible, and by the much longer larval postgenal cleft. It appears also to be related to the subgenus *Xenosimulium* sgen. n. from Madagascar, in which the larval mandible shows similar modifications from the norm in the enlargement of the comb-teeth and relative reduction of the apical teeth and in extreme development of the primary brush.

There are no obvious affinities between *Freemanellum* and any Holarctic or Oriento-Australasian segregate of *Simulium*, but there appears to be some relationship with certain forms in South America that have a strong resemblance to the Ethiopian *Anasolen* species. The Neotropical *Simulium lahillei* Paterson & Shannon, type-species of the subgenus *Grenierella* Vargas & Diaz Najera, has many characters in common with (and to a large extent intermediate between) those of *Freemanellum* and *Anasolen* from the Ethiopian Region : in *lahillei* the male styles are longer than the coxites, the female paraprocts are enlarged and the larval postgenal cleft is elongate-oval recalling the characters found in *Freemanellum*, but the female tarsal claw-teeth are very small, there are twelve pointed branches in the pupal gill and the hypostomium of the larva has a straight apical row of small but well formed teeth, these characters being much as in *Anasolen*.

The species of *Freemanellum* are exceptional among African black-flies in having a predominantly reddish brown colour, especially rich on the scutum of the male ; in this feature, too, they resemble *S. (Grenierella) lahillei* from South America in which the thorax is distinctly orange to reddish brown. A detailed description of *lahillei* is given by Wygodzinsky (1949).

At the present time little material is available of *Freemanellum* species and only *berghei* Fain and *debegene* de Meillon are so far known in the larval stage (the foregoing diagnosis may therefore need modification when more material and all stages of all species are known). The larvae of both *berghei* and *debegene* have a rather exceptional mandible: the primary brush is extraordinarily produced apically and very conspicuous beyond the end of the mandibular body, as shown for *berghei* in Text-fig. 295; the brush in *debegene* is also produced but appears to be strongly curved round in a similar way to that of *S. (Xenosimulium) imerinae* (Text-fig. 296); in both species the comb-teeth are excessively large and the main apical teeth reduced so that they are no larger than the comb-teeth (Text-fig. 301). These larval mandibular characters help in distinguishing the larvae of *Freemanellum* from those of *Anasolen* and *Metomphalus*, with which they sometimes occur in cascading streams.

The distribution of subgenus *Freemanellum* is disjunct on present evidence, there being a main centre of distribution along the south-eastern side of the African continent (Map 8) and an isolate in the extreme west of West Africa. The West African locality is based upon a single pupa, apparently of *S.(F.) debegene* de Meillon (specimen in BMNH: examined), recorded by Garms & Post (1967) from Guinea. It is unlikely that such an extreme break in distribution really exists, and species of the subgenus are here presumed to occur in intermediate areas although they have not yet been discovered there\*.

Included taxa. *Simulium (Freemanellum) berghei* Fain; *S.(F.) debegene* de Meillon; *S.(F.) empopomae* de Meillon; *S.(F.) hessei* Gibbins; *S.(F.) hirsutilateris* de Meillon.

### Subgenus *WILHELMIA* Enderlein

*Wilhelmia* Enderlein, 1921: 199. Type-species: *Atractocera lineata* Meigen, 1804, by original designation.

Diagnosis. ♂♀: Basal section of radius haired. Pleural membrane haired. Katepisternum bare. Fore tarsus slender, fore basitarsus six or seven times as long as its greatest breadth. Hind basitarsus 1.15–1.25 times as long as remainder of hind tarsus (cf. *Metomphalus*). ♀: cibarium unarmed. Tarsal claws very enlarged (about two-thirds as long as third fore tarsal segment and longer than width of this segment), without basal tooth. Scutum greyish with three fine longitudinal dark lines meeting posteriorly to form lyre-shaped mark (Text-fig. 72). Abdomen uniformly silvery-scaled. Seventh sternite undeveloped. Gonapophyses forming slender curled acuminate processes. Paraprocts normal. Spermatheca without internal hairs. ♂: scutum greyish black to velvety black with or without a pair of large silvery grey triangular areas anterolaterally. Genitalia with very small styles and enlarged coxites, style usually folded down against body of coxite, with one apical spinule; coxite at least slightly produced beyond base of style; ventral plate subtriangular in form with elongate basal arms which are usually widely divergent, body of plate not toothed; median sclerite toothed, usually bifurcate or clubbed apically, sometimes rounded; parameres long and slender, parameral hooks numerous. *Pupa*: Gill formed of enlarged thin-walled unornamented tubular basal arms, oriented dorso-ventrally, between which arise medially several (usually 6) tubular filaments directed forwards (Text-fig. 207); medial series of branches sometimes short and stout. Abdominal segments 6–9 dorsally without spine-combs. Cocoon with well formed neck, shoe-shaped. *Larva*: Head and

\* See Appendix

cephalic fans normal. Hypostomium with usual nine apical teeth, these short and blunt ; 3-6 setae in each hypostomial row, rows divergent behind from lateral margins of hypostomium. Head-spots positive, usually very distinct and not lost in general pigmentation. Postgenal cleft large, much longer than postgenal bridge, broadly and bluntly sagittate or subcordate. Mandible normal, first three comb-teeth evenly decreasing, two serrations. Antenna short, with four segments. Thoracic cuticle bare. Abdominal cuticle appearing bare but posterodorsally with a few very minute deeply trifid setae. Abdominal shape normal. Ventral papillae absent. Accessory sclerites absent. Rectal scales absent. Rectal gills without secondary lobules. Posterior circlet with about 90-120 rows of 17-30 hooks.

Distribution. Confined to the Palaearctic Region, and well represented in the Mediterranean area and the Middle East. The distribution includes the British Isles, Japan, Iran and West Pakistan but excludes Iceland ; the range may overlap the fringes of the Oriental Region in Kashmir and West Pakistan proper. North African distribution is shown on Map 9.

Discussion. *Wilhelmia* forms an isolated subgenus in the Palaearctic *Simulium* fauna having little or no apparent affinity with any other segregate in the region. The formation of the pupal gill, the unique type of male hypopygium, the enlarged claws and slender elongate gonapophyses of the female, all set the group apart from the rest of the Palaearctic fauna ; on the other hand some of these characters together with the characters of the larvae indicate almost certain phyletic affinity with the endemic Ethiopian subgenera *Metomphalus* and *Edwardsellum*. The three segregates taken together seem to form a natural group of subgenera within *Simulium* having the following characters in common : Basal section of radius haired ; styles of male genitalia small in relation to large coxites ; body of ventral plate typically subtriangular with divergent basal arms ; scutum of female with at least a trace of a lyrate dark mark (resembling Text-fig. 72) ; no trace of sclerotized seventh sternite on female abdomen ; gonapophyses of female terminalia drawn out into thin pointed processes, often curled ; cocoon with neck ; pupal gill composed of large thin-walled basal arms with stout tubular filaments arising between them ; dorsum of pupal abdomen without spine-combs ; postgenal cleft of larval head large ; larval hypostomium with short blunt teeth and the rows of hypostomial setae diverging posteriorly from the margin of the hypostomium ; larval antenna about equal in length to stem of cephalic fan ; larval abdomen without ventral papillae ; typically fast water forms with mammalophilic females.

Stone (1963) placed the names *Edwardsellum* and *Metomphalus* as synonyms of *Wilhelmia*, but it is here considered preferable to treat the three as closely related but separate subgenera. Further discussion of the reasons for this is given under *Edwardsellum*.

The subgenus *Wilhelmia* forms a predominant component in the *Simulium* fauna of the Mediterranean basin and its islands ; on the African continent it ranges from Morocco to Tunisia. Two species, *canariense* and *pseudequinum*, that belong in the subgenus have been described from the Canary Islands by Séguy (1921) : the descriptions are of adults only and the identity of these species is uncertain, but it is likely that at least one of the names applies to (and has priority over) *mediterraneum* Puri. Adequate recognition of species in the subgenus *Wilhelmia* requires the pupal

stage as well as the male adults, and many supposed species or subspecies of doubtful validity have been described that are based upon small differences in pupal gill form or the structures of the male genitalia.

Rubzov (1959-1964 : 392-416) recognizes three species-groups (*equinum*-group, *salopiense*-group, and *sergenti*-group) in *Wilhelmia*, but it is here considered that there is such a homogeneity among the constituent elements in the subgenus (genus *sensu* Rubzov), whatever their taxonomic ranking in status, that no species-group classification is required ; I therefore recognize no species-groups in the present work.

Enderlein (1921, 1922, 1925, 1930) assigned several non-Palaeartic species to *Wilhelmia* but later removed some of them to other genera. None of these belong in the subgenus *Wilhelmia* as now understood, but for convenient reference the species involved are given in the following list with the subgenus to which they now belong indicated in brackets after the specific name : *exiguum* Roubaud (*Notolepria* Enderlein) ; *hippovororum* Malloch (*Hemicnetha* Enderlein) ; *mallochi* Enderlein (? *Simulium* Latreille s. str.) ; *pictipes* Hagen (*Hagenomyia* Shewell) ; *pygmaea* Enderlein (*Morops* Enderlein) ; *vittatum* Zetterstedt (*Psilozia* Enderlein) ; *wolffhuegeli* Enderlein (? *Psilopelmia* Enderlein). Enderlein (1930 : 93) placed *australienensis* Schiner in *Wilhelmia*, but this a New Zealand species now belonging in the genus *Austrosimulium* Tonnoir.

Included taxa. The subgenus includes all species and subspecies placed in *Wilhelmia* in Rubzov's (1959-1964) monograph of Palaeartic Simuliidae, except for *Simulium guimari* Becker (which, following the lectotype designation made for this species by Crosskey (1965b : 669), belongs in the subgenus *Eusimulium*). In addition it includes *Simulium (Wilhelmia) zellandense* Davies, 1966, and *Simulium (Wilhelmia) balcanicum* ssp. *severinense* (Dinulescu, 1966) which have been described since the completion of Rubzov's monograph.

The included taxa in the purview of the present paper are from North Africa and the Canary Islands and are : *Simulium (Wilhelmia) ariasi* Séguy ; *S.(W.) barbaricum* Séguy ; *S.(W.) canariense* Séguy ; *S.(W.) equinum* (Linnaeus) ; *S.(W.) mediterraneum* Puri ; *S.(W.) pseudequinum* Séguy ; *S.(W.) quadrifila* Grenier, Faure & Laurent ; *S.(W.) sergenti* Edwards. [Note : it is almost certain that the names of some of these taxa recorded or described from the North African area are synonyms of each other.]

### Subgenus *METOMPHALUS* Enderlein

*Metomphalus* Enderlein, 1935 : 361. Type-species : *Metomphalus caffer* Enderlein, 1935 [= *Simulium medusaeformis* Pomeroy, 1920], by original designation.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane bare (some exceptions). Katepisternum bare. Fore tarsus not or slightly dilated, fore basitarsus five to seven times as long as its greatest breadth. Hind basitarsus 1.4-1.6 times as long as remainder of hind tarsus (cf. *Wilhelmia*). ♀ : cibarium unarmed or occasionally with small denticles between cornuae. Tarsal claws without basal tooth. Scutum with inconspicuous dark pattern, usually in form of lyrate mark. Abdomen evenly covered with scales. Seventh sternite undeveloped. Gonapophyses slender and pointed, usually curled but sometimes long and straight. Paraprocts

normal. Spermatheca with internal hairs, surface smooth. ♂ : scutum with bold black and silvery grey pattern or at least with an anterior pair of indefinite subtriangular silvery areas. Genitalia with small tapering or truncate styles much shorter than coxite (Text-fig. 152), style not folded down against body of coxite ; style with one apical spinule (except *wellmanni*) ; coxite sometimes produced beyond base of style ; ventral plate complex, body usually subtriangular and toothed apically, basal arms divergent ; median sclerite usually simple and parallel-sided, sometimes bifurcate, end sometimes frayed but not toothed ; parameres long and slender, parameral hooks numerous. *Pupa* : Gill formed of large thin-walled tubes or of stout primary branches bearing fine secondary filaments, rarely entirely filamentous. Abdomen with normal complement of hooks (except some forms lacking hooks ventrally on segment 5) ; segments 6-9 dorsally without spine-combs. Cocoon with well formed neck, shoe-shaped (except *albivirgutum*). *Larva* : Head and cephalic fans normal. Hypostomium with usual row of nine apical teeth, teeth short and blunt ; 3-10 setae in each hypostomial row, rows divergent behind from lateral margins of hypostomium. Head-spots positive, sometimes indistinct. Postgenal cleft large, much longer than postgenal bridge, usually rounded or bluntly sagittate. Mandible normal, comb-teeth regularly decreasing in size, two serrations. Antenna short, with four segments. Thoracic cuticle bare (one exception). Abdominal shape varied, cuticle with scales or minute spinous hairs. Ventral papillae absent. No accessory sclerites. Rectal scales present. Rectal gills simple or compound. Posterior cirlet with 110-220 rows of 18-49 hooks.

**Bionomy.** Eggs clustered, adhered to substrate. Larval and pupal stages non-phoretic ; on vegetation and rock-surfaces or stones, mainly in fast waters of rapids and cascades. Female mammalophilic, including anthropophilic.

**Distribution.** Widespread throughout the Ethiopian Region, including southern Arabia (Map 9). The subgenus is absent from the Malagasy Region, unless *Simulium gyas* de Meillon (at present known only from the pupal stage) should later prove to be assignable to *Metomphalus*.

**Discussion.** This large endemic Ethiopian subgenus is very distinctive and has no apparent affinity with any segregate of the *Simulium* s.l. fauna in either South America or the Oriento-Australasian Regions. It appears to be most closely allied to the Palaearctic (including North African) subgenus *Wilhelmia*, and Rubzov (1940 : 126-127) in his earlier work placed one of the species, *S. medusaeforme* Pomeroy, in *Wilhelmia*. It is now clear that the species of *Metomphalus* differ considerably and rather consistently from those of *Wilhelmia* in both sexes and in the larval stage (though not significantly in the pupal stage) and that for a balanced classification within *Simulium* both groups should be recognized as subgenera. The female of *Wilhelmia* differs from that of *Metomphalus* (and in fact from that of all other segregates of *Simulium* s.l.) in the exceptionally enlarged claws, and the male by the unique and characteristic structure of the genitalia (again unlike that of any other *Simulium* s.l.) : other differences include most notably the condition of the pleural membrane (always haired in *Wilhelmia*, almost always bare in *Metomphalus*) and the vestiture of the larval abdomen (deeply divided trifid hairs in *Wilhelmia*, scales or simple spinous setae in *Metomphalus*). The subgenus *Metomphalus* as here treated corresponds with the *medusaeforme*-group of Freeman & de Meillon (1953) with *S. damnosum* Theobald excluded (see *Edwardsellum*).

The immature stages of some species of *Metomphalus* may occur in slowly-moving water, but those of most forms characteristically occur in fast-moving turbulent

streams, in rapids or in rock cascades, where the subgenus usually forms the dominant component in the simuliid fauna throughout Ethiopian Africa ; ecologically the subgenus *Metomphalus* may be regarded in this area as the fast-water counterpart to the slow-water subgenus *Pomeroyellum* (although the latter subgenus does contain a few torrenticolous species that may cohabit in the same watercourses with species of *Metomphalus*). A notable feature in this subgenus is the extreme abundance in which the juveniles of many species occur, larvae and pupae sometimes densely coating the smooth submerged rock surfaces of cascades or hanging in thick masses on trailing roots.

The species of *Metomphalus* fall into three main groups distinguishable by the characters given in the key and definitions below.

KEY TO THE SPECIES-GROUPS OF THE SUBGENUS *METOMPHALUS*

- 1 Larva with dense covering of large conspicuous scales on abdomen and dorsum of thorax ; postgenal cleft subelliptical (Text-fig. 259). Cocoon without definite neck. Pupal gill filamentous (Text-fig. 214). Body of ♂ ventral plate subtriangular and bordered with strong spines (Text-fig. 117) . . . . . **albivirgatum-group** (p. 98)
- Larva with thoracic cuticle bare and abdominal cuticle with minute inconspicuous hairs or scales only on posterodorsal region ; postgenal cleft not of this shape. Cocoon with well developed neck. Pupal gill with stout primary branches and fine secondary filaments or with fat tubular branches. ♂ ventral plate not of this form . . . . . 2
- 2 Pupal abdomen with the normal pair of hooks each side ventrally on segment 5. Pupal gill with basal arms (Text-figs. 211-213). Larval abdomen posterodorsally with sparse spinous hairs (Text-fig. 227) ; postgenal cleft subcordate or bluntly sagittate (Text-figs. 256-258). ♂ scutum without bold pattern, usually with indefinite pair of silvery triangles anteriorly . . . . . **medusaeforme-group** (p. 100)
- Pupal abdomen without hooks ventrally on segment 5 or with a single minute hooklet on each side. Pupal gill without basal arms (Text-figs. 215, 216). Larval abdomen posterodorsally with blunt flattened scales (Text-fig.-229) ; postgenal cleft subcircular (Text-fig. 260). ♂ scutum often with very bold black and silver-grey pattern . . . . . **bovis-group** (p. 99)

**albivirgatum-group.** Small species, wing length 1.7-2.3 mm. ♂ scutum with anterior pair of subtriangular brilliant silver-white scaled patches. ♂ ventral plate complex, forming right-angle in profile (Text-fig. 135), body of plate with strong marginal thorns, subtriangular. ♀ cibarium unarmed. Pupal gill of 25-40 simple filaments coalesced only at extreme base. Pupal abdomen with usual two hooks each side on venter of segment 5. Cocoon without neck, although usually with a very narrow woven band connecting or almost connecting the two anteroventral corners of the cocoon. Larval head elongate, postgenal cleft elongate subelliptical ; hypostomium with two of the lateral serrations formed into rather definite teeth outside the main anterior row of nine teeth (Text-fig. 281). Larval thoracic cuticle dorsally with large scales. Larval abdomen of unusual shape (Text-fig. 287), not noticeably swollen posteriorly, first few segments sometimes expanded mediodorsally (appearance of such swelling emphasized by clustering of the scales) ; almost whole abdomen densely covered with large scales.

At present this group contains only one remarkable species that differs from all other African *Simulium* s.l. except those in the subgenus *Edwardsellum* by having a dense vestiture of large scales (immediately obvious with low-power magnification) over the thorax and abdomen ; on this and other characters of the larva it could well be placed in a separate subgenus, but the adult and pupal characters conform closely with those of *Metomphalus* and it appears best to assign it to this subgenus.

The undeveloped neck to the cocoon, also atypical for *Metomphalus*, may be a character associated with the fact that the species breeds often in rather slow waters.

Included taxa : *Simulium* (*Metomphalus*) *albivirgulatum* Wanson & Henrard.

**bovis-group.** Small species, wing length 1.6–2.3 mm. ♂ scutum without pattern or with very bold conspicuous pattern of black and pale silver-grey, as in Text-fig. 76 or with the centre vitta merging with lateral black vittae. ♂ ventral plate of varied form, usually body of plate subtriangular with divergent basal arms, or broadly transverse with parallel basal arms (Text-fig. 115) ; coxite often produced as a narrow elongate process beyond base of style. ♀ cibarium unarmed. Pupal gill with stout primary filaments and fine slender secondaries, without basal arms. Pupal abdomen unusual, lacking hooks or showing only one minute inconspicuous hooklet each side on segment 5. Cocoon with neck. Postgenal cleft very large and rounded. Hypostomium with normal teeth (Text-fig. 280), 4–5 setae in each hypostomial row. Larval thoracic cuticle bare, abdominal cuticle with minute flattened truncate scales posterodorsally and abdominal shape as in Text-fig. 228.

This group contains species that are most uniform in the immature stages but more diverse in the characters of the male and female terminalia, particularly because of the inclusion of *S. wellmanni* in the group. This species differs from all other African *Simulium* s.l. in possessing multiple spinules on the style of the ♂ genitalia (Text-fig. 153) and from other members of the *bovis*-group by having the median sclerite deeply cleft and the apical prolongation of the coxite equal in length to the style : characters of the female, larva and pupa of *wellmanni*, however, undoubtedly indicate close affinity of this species with *bovis* and its immediate allies (for description of the larva of *wellmanni* see Grenier *et al.* (1961 : 1139)). Until recently *S. wellmanni* also appeared unique on account of the long straight very slender and backwardly-directed gonapophyses of the female terminalia (Text-fig. 160) but *S. janzi* has been shown to have similar gonapophyses (figured by Marini de Araújo Abreu (1961 : 84)) ; the male of *S. janzi* has a complex ventral plate essentially of transverse shape like that of *wellmanni*, but has only one apical spinule on the style and a much shorter coxite process, thus providing an aggregate of characters intermediate between those of *wellmanni* and those of *bovis*. The form of the pupal gill of *janzi* also falls between that of *wellmanni* and that of *bovis*, and supports the inclusion of *wellmanni* in the *bovis*-group.

The larvae of the *bovis*-group species are small and usually very pale, with little body mottling and with the head capsule often creamy white with almost no pigmentation ; the membranous area of the large rounded postgenal cleft tends to be inconspicuous against the pale head colour (in contrast to the larvae of the *medusaeforme*-group in which pigmentation is well marked and the postgenal cleft conspicuous). Body form in the larvae tends to resemble that occurring in the subgenus *Pomeroyellum*, but without ventral papillae (Text-fig. 228) ; the scales of the abdomen are minute and inconspicuous, so that the larvae appear bare at first glance, unlike the very large abdominal scales found in the *albivirgulatum*-group of *Metomphalus* or the *cervicornutum*-group of *Pomeroyellum* (Text-fig. 224) that are immediately obvious.<sup>1</sup>

<sup>1</sup> McCrae (personal communication) has now obtained *bovis*-group larvae from Ethiopia, that appear to be those of *S. fragai* or a very closely related new species, in which abdominal scaling is obvious on much of the dorsum of the abdomen and around the sides of the terminal segments.

The scutum of the male in this group varies from mainly velvety black with some silvery scaling laterally and posteriorly, and with silvery triangles anteriorly, to a very well defined black and silver pattern in which three separated black vittae occur : the latter form is particularly well developed in *S. chutteri* (Text-fig. 76) and resembles the pattern found in males of *Edwardsellum* (Text-fig. 77).

Included taxa. *Simulium* (*Metomphalus*) *arnoldi* Gibbins ; *S.(M.) bovis* de Meillon ; *S.(M.) chutteri* Lewis ; *S.(M.) fragai* Marini de Araújo Abreu ; *S.(M.) janzi* Marini de Araújo Abreu ; *S.(M.) wellmanni* Roubaud.

**medusaeforme-group.** Medium-sized to large species, wing length 2.4–3.6 mm. ♂ scutum without very definite pattern, only with pair of anterior silvery triangles (often indistinct) in addition to pale-scaled margins. ♂ ventral plate toothed apically, with widely divergent basal arms ; coxite not produced beyond base of style. ♀ cibarium unarmed or weakly toothed between cornuae. Pupal gill with basal arms, with one type of large inflated thin-walled filaments or with stout primary filaments bearing fine secondaries. Pupal abdomen with the normal pair of hooks each side ventrally on segment 5. Cocoon with neck. Postgenal cleft pentagonal, subcordate or truncate-sagittate. Hypostomial teeth normal (Text-figs. 278 & 279), 4–10 (usually 6–8) setae in hypostomial row. Larval thoracic cuticle bare, abdominal cuticle with minute sparse spinous hairs. Larval abdomen usually expanded gradually when seen in profile and contracting suddenly to posterior circlet (Text-fig. 226).

This is the largest species-group of *Metomphalus* and contains several forms characteristic of high-altitude mountain streams, often occurring together with species of subgenus *Anasolen* in swift cold cascades. The species are rather uniform in the males (including male genital characters), females, and larvae, but the pupal gill shows throughout the group a transition from forms with the filaments of two quite distinct kinds (stiff dark primary branches and slender thread-like secondary filaments) to forms with a single kind of thin-walled dilated filament—generally somewhat sausage-like or banana-like. The larval head is usually strongly pigmented, sometimes to such an extent that the dark head-spots are almost lost among the general dark brown infuscation, and the postgenal cleft is very conspicuous (in some forms a lightly pigmented area extends forwards medially from the cleft to the base of the hypostomium, making it appear as though the cleft itself is drawn out anteriorly). The general appearance of the larvae is closely similar to that of *Anasolen* larvae, but the small postgenal cleft in the latter distinguishes them from larvae of the *medusaeforme*-group ; larvae are less easy to distinguish from those of the subgenus *Freemanellum*, but appear to be consistently separable in the two groups by the brush structure of the apex of the mandible (cf. Text-figs. 294 and 295). A striking larval mandibular feature in many species of the *medusaeforme*-group is the unusual elongation of the distal one of the pair of serrations (as shown in Text-fig. 300), a character found particularly in *vorax* and its immediate allies. A remarkable feature of these species, not found in other Ethiopian *Simulium*, is the presence of small but distinct teeth in the female cibarium.

Two species of the *medusaeforme*-group (*S. letabum* and *S. natalense*, possibly also *S. fragai*) have the pleural membrane haired and thereby differ from other *Metomphalus* species, and a few species of the group (mainly *S. vorax* and allies) have

the hind basitarsus of the male distinctly dilated : in the *albivirgulatum*-group and the *bovis*-group the male hind basitarsus is always slender and parallel-sided.

Included taxa. *Simulium* (*Metomphalus*) *africanum* Gibbins ; *S.(M.) cavum* Gibbins ; *S.(M.) colasbelcourti* Grenier & Ovazza ; *S.(M.) futaense* Garms & Post ; *S.(M.) hargreavesi* Gibbins ; *S.(M.) letabum* de Meillon ; *S.(M.) medusaeforme* Pomeroy ; *S.(M.) natalense* de Meillon ; *S.(M.) ruandae* Fain ; *S.(M.) taylori* Gibbins ; *S.(M.) touffeum* Gibbins ; *S.(M.) vorax* Pomeroy ; *S.(M.) zombaense* Freeman & de Meillon.

In addition the nomenclaturally unavailable form name *angolensis* has been applied by Marini de Araújo Abreu (1961) to a taxon of this group.

Ungrouped species : *Simulium gyas* de Meillon.

The species *Simulium gyas* de Meillon from Madagascar may belong in the subgenus *Metomphalus*, but at present it is known only from the larval and pupal stages and there is insufficient evidence for definite assignment to this subgenus. The cocoon in this species is reduced, covering only the pupal abdomen and posterodorsal part of the thorax, but the abdominal onchotaxy of the pupa conforms with that of *Metomphalus* : the pupal gill (Text-fig. 208) has six stiff branches arising in pairs, unlike any other African species, but suggesting some possible relationship with *S. hargreavesi* Gibbins. If a form such as *hargreavesi* lost the fine secondary filaments of the gill so that only the main primary arms were retained it would resemble *gyas* in gill form, so that the six branches existing in *gyas* could possibly be homologous with the primary gill filaments in *hargreavesi* and its allies.

This suggestion of possible affinity with *hargreavesi* is supported by the larval characters of *gyas* which have been described and figured by Grenier and Doucet (1949) under the name *Simulium* sp. M<sub>6</sub> ; the form of the postgenal cleft, the mandible, the cuticular spines of the abdomen, and the hypostomium and its setae all conform with the larval characters of the *medusaeforme*-group of *Metomphalus*. *Simulium gyas* therefore, on the basis of its known stages, shows most affinity with subgenus *Metomphalus* and could tentatively be assigned to this subgenus pending discovery of the adult stage.

### Subgenus **EDWARDSSELLUM** Enderlein

*Edwardssellum* Enderlein, 1921 : 199. Type-species : *Simulium damnosum* Theobald, 1903, by original designation.

Diagnosis. ♂♀ : Basal section of radius haired. Pleural membrane bare. Katepisternum bare. Fore tarsus greatly dilated, fore basitarsis 3.6-4.2 times as long as its greatest breadth, with dorsal hair crest. ♀ : cibarium unarmed. Tarsal claws with basal tooth, sometimes small. Scutum black with bluish grey bloom and very inconspicuous pattern of three fine dark longitudinal lines. Abdomen densely silver-scaled on segment 2 and with lateral and ventral tufts of silvery white scales on segments 2-5, dorsum of segments 5-9 shining black with only sparse erect hairs. Seventh sternite undeveloped. Gonapophyses attenuate, usually curled acuminate. Paraprocts normal. Spermatheca with internal hairs, surface smooth. ♂ : scutum with bold black and silvery grey pattern. Genitalia with small tapering styles shorter than coxite ;

style with one apical spinule ; coxite at least slightly produced beyond base of style ; ventral plate complex, basal arms divergent, strongly arched in profile, body of plate more or less toothed ; median sclerite with biramous apex at right angles to body of sclerite or straight and cleft apically, not toothed ; parameres narrow, parameral hooks numerous. *Pupa* : Gill formed of large thin-walled tubes comprised of a pair of basal arms and six or nine filaments arising between these. Abdomen with normal onchotaxy ; segments 6-9 without spine-combs dorsally. Cocoon with well formed neck, shoe-shaped. *Larva* : Head and cephalic fans normal. Hypostomium with usual nine apical teeth, these short and blunt (Text-fig. 282) ; 4-6 setae in each hypostomial row, rows divergent behind from lateral margins of hypostomium. Head-spots positive, head often heavily pigmented. Postgenal cleft very large, rounded-cordate or almost circular, occupying most of venter of head, postgenal bridge very reduced in mid-line so that cleft may nearly reach base of hypostomium. Mandible normal, first three comb-teeth subequal, two serrations (smaller one sometimes missing). Antenna short, with four segments. Thoracic cuticle (including that of proleg) and abdominal cuticle extensively covered with flattened lanceolate or ovate scales. Abdomen with paired dorsolateral swellings or subconical prominences on first five segments (Text-fig. 230), these especially conspicuous even when small through aggregation of dark scales. Ventral papillae absent. Accessory sclerites absent or represented by small sclerotized platelets. Rectal scales present or (apparently) sometimes absent. Rectal gills compound, each lobe with numerous slender finger-like secondary lobules. Posterior circlet with 120-170 rows of 18-45 hooks.

**Bionomy.** Eggs clustered, adhered to substrate. Larval and pupal stages non-phoretic ; most often attached to trailing vegetation in rapids of moderate to large size rivers, less commonly in streams or on stones and rock surfaces. Attachment of eggs, larvae and pupae very characteristically occurs on grasses dipping into fast broken water. Female mammalophilic, including anthropophilic ; also ornithophilic.

**Distribution.** Widespread in the Ethiopian Region (Map 10), excluding southern Arabia. The range extends further northwards along the Nile valley than in other subgenera (except *Byssodon*) and reaches as far as the Second Cataract of the Nile near the Egyptian border with Sudan ; it includes also the island of Fernando Po in the Gulf of Guinea. The subgenus is absent from the Malagasy Region.

**Discussion.** *Edwardsellum* is the most easily recognized subgenus of *Simulium* in the Ethiopian Region because of the distinctive larvae, with their striking covering of scales and paired swellings or tubercles on the first five segments of the abdomen (Text-fig. 230), and because of the enlarged fore tarsi of the adults (Text-fig. 82). No similar larvae occur in the Ethiopian fauna, and the only other Ethiopian subgenus with dilated fore tarsi is *Phoretomyia* ; males of *Edwardsellum* can easily be distinguished, however, from those of *Phoretomyia* by the bold black and silver-grey pattern on the scutum (usually much as in Text-fig. 77) and both sexes are very different in the terminalia. There is certainly no relationship between these subgenera, and a dilated fore tarsus is clearly a character derived independently in the two groups.

The subgenus *Edwardsellum* has no affinity with, or no close resemblance to, any New World subgenus or to any of the subgenera occurring in the Oriento-Australasian Regions. There is a superficial similarity between the males of *Edwardsellum* and those of some Oriental species of *Simulium* s.l. placed by Edwards (1934) in his

Group I, Sub-group B, particularly *S. nebulicolum* Edwards, *S. iridescens* de Meijere, and *S. nobile* de Meijere ; these forms have a dilated fore tarsus and a bold black and grey pattern to the male scutum, but the basal section of the radius is bare and the male hypopygium is of the type found in *Simulium* s. str., and there is clearly no close relationship between them and *Edwardsellum*. Although the Oriental *Simulium* fauna has not been studied in detail it is certain that most of the species in this region that lack hairs on the base of the radius and have heavy elongate male styles are assignable to the subgenus *Simulium* s. str., and that they have little or no relationship with the Afro-Palaeartic group of subgenera associated with *Wilhelmia* (in which *Edwardsellum* clearly fits).

The characters of the pupa, the larval head, the male genitalia and the gonapophyses of the female terminalia all closely resemble those of the subgenus *Metomphalus*, and to a lesser extent of *Wilhelmia*, and the phyletic affinities of *Edwardsellum* lie with these subgenera. Freeman & de Meillon (1953) placed *Simulium damnosum*, the type-species of *Edwardsellum*, in their *medusaeforme*-group (the typical group of the subgenus *Metomphalus*) and it would be possible to regard the species of *Edwardsellum* as constituting a species-group in the same subgenus as the *medusaeforme*-group and the *bovis*-group. If this course was adopted the valid name for the composite subgenus so recognized would be *Edwardsellum* Enderlein, 1921 (with priority over *Metomphalus* Enderlein, 1935). However, it appears preferable to rank *Edwardsellum* and *Metomphalus* as separate subgenera because of the major differences in the larval and adult stages, especially as it would be difficult to formulate any satisfactory diagnosis of the resultant group if the two concepts were merged.

Both the subgenera *Edwardsellum* and *Metomphalus* are closely related to *Wilhelmia*, as is especially evident from the pupal stage (cf. gill form, especially the basal arms, in Text-fig. 207 with that in Text-figs. 209, 210 and 212), but not so closely as to justify the synonymy of the three names : for a balanced classification on a world basis the two Ethiopian subgenera require to be maintained as named entities, equivalent in rank to the Palaeartic subgenus *Wilhelmia*. I therefore do not follow Stone (1963 : 6, 12, 22) in treating the names as synonyms, or Rubzov (1962 : 1500-1501) in treating *Edwardsellum* as a full genus to include all the species here placed in the subgenus *Metomphalus* as well as those placed in *Edwardsellum*, but prefer to recognize three segregates of equal subgeneric status. Distinctions between *Metomphalus* and *Wilhelmia* are discussed under *Metomphalus* : the following summary of characters shows the main differences between *Edwardsellum* and *Wilhelmia* :—

*Edwardsellum*. Pleural membrane bare. Tarsal claws of ♀ toothed, not enlarged. Scutum of ♂ with black and silver-grey pattern, scutum of ♀ bluish black with very indistinct dark lines. ♂ ventral plate toothed, complex shapes ; median sclerite not toothed apically. Larval thorax and abdomen with vestiture of simple scales ; first five abdominal segments with paired dorsal tubercles. Rectal gills with secondary lobules.

*Wilhelmia*. Pleural membrane haired. Tarsal claws of ♀ simple, greatly enlarged. Scutum of ♂ without bold black and grey pattern, scutum of ♀ pale greyish with conspicuous dark lyrate mark (Text-fig. 72). ♂ ventral plate not toothed, excavate-subtriangular (Text-fig. 113) ;

median sclerite toothed apically. Larval thorax bare, abdomen with sparse very minute divided hairs and normal shape (without dorsal tubercles). Rectal gills without secondary lobules.

At present the subgenus *Edwardsellum* contains three species ; two of these are known only from Angola, but the other is *Simulium damnosum* Theobald, the most serious man-biting Simuliid in tropical Africa and the main vector of human onchocerciasis in Africa (Map 10 shows the distribution of this important vector species since it occurs in all localities for which the black circle symbols are shown). The number of species in *Edwardsellum* may be much increased as the result of current and future work on *S. damnosum*, since it is possible (and by some workers regarded as already proven) that this species is a complex of sibling species, some of which are primarily anthropophilic and others non-anthropophilic—a difference in feeding habits with a direct bearing on the transmission of human onchocerciasis, and therefore of more than academic interest. Particularly clear-cut distinctions in feeding habits exist in different localities of *S. damnosum* in Uganda, anthropophily being the norm in some and non-anthropophily in others, and Dunbar (1966) claims that at least four sibling species are represented in the '*S. damnosum*' populations of Uganda : names available in nomenclature have not been given to the different sibling segregates, but Dunbar correctly points out that the restricted name *damnosum* would apply to the anthropophilic form occurring in the Victoria Nile near Jinja whence the type-material of *damnosum* originated.

Dunbar's sibling species have been distinguished solely on cytological differences found in the giant polytene chromosomes of the salivary glands of *S. damnosum* larvae from different locations, each sibling being recognized by inversions imposed on the same basic banding pattern sequence ; the characters used in differentiating the siblings are micromorphological ones, the genetical significance of which is uncertain. No experimental evidence exists to support the supposition that the cytologically distinguishable entities (of which nine are now known from different parts of Africa) within *S. damnosum* are biologically distinct species, and it may be premature to assume that they are. So far the various components of *S. damnosum* have been shown to differ only in the larval chromosome characters, and no correlated differences have yet been demonstrated in external larval characters or in the morphology of other stages. Nonetheless the subgenus *Edwardsellum* must be looked upon as composed of a minimum of three species, with the possibility or likelihood that several others exist : if so it is possible that Enderlein's names applied to *S. damnosum* may be recovered from synonymy.

Included taxa. *Simulium* (*Edwardsellum*) *damnosum* Theobald and associated supposed sibling species, at present unnamed (see above) ; *S.(E.) machadoi* Luna de Carvalho ; *S.(E.) vilhenai* Luna de Carvalho.

#### Subgenus **TETISIMULIUM** Rubzov

*Tetisimulium* Rubzov, 1963 : 497. Type-species: *Melusina bezzii* Corti, 1914, by original designation.

Diagnosis. ♂♀ : Basal section of radius bare. Pleural membrane haired. Katepisternum

bare. Fore tarsus slender, fore basitarsus 6.75–8.5 times as long as its greatest breadth. ♀ : cibarium toothed between cornuae. Tarsal claws with minute pointed basal tooth. Scutum pale ashy grey with three broad dark vittae. Abdomen patterned, pale grey pruinose with three blackish brown longitudinal bands formed by subquadrate dark marks on dorsum of segments 3–5 and median dark vitta extending to tergites 6 or 7. Seventh sternite well developed, rather strongly haired. Gonapophyses slightly produced and rounded, concave on inner margin. Paraprocts normal or slightly produced downwards. Spermatheca without definite pattern or internal hairs. ♂ : scutum with black and silvery pattern, sometimes a broad black median band with shorter broad black sublateral vittae that more or less merge with median vitta, sometimes extensively black with silver shoulder marks and greyish pruinose sides and hind margin. Genitalia with very large heavy elongate subparallel-sided styles and short broad coxites, style very much longer than coxite and with one apical spinule ; ventral plate small and Y-shaped with toothed and haired body and widely divergent basal arms, without beak-like process in profile ; median sclerite elongate subovate, sometimes acuminate basally and usually widened and slightly cleft apically ; parameres large, elongate subtriangular, parameral hooks very numerous. *Pupa* : Gill filamentous, 6 or 8 long slender filaments arising near base and directed forwards, gill shorter than pupal body. Abdominal onchotaxy normal, fourth segment ventrally without supernumerary hook each side, segment 2 dorsally with three or four minute spinous hooklets each side, a few long hairs on the segments laterally and lateroventrally ; dorsal spine-combs only on segment 8, only few stout spines either side on well sclerotized band. Cocoon shoe-shaped, fenestrate anteriorly and especially on neck, the openings numerous and irregular. *Larva* : Head and cephalic fans normal. Hypostomium with usual nine apical teeth, median and corner teeth moderately to strongly prominent ; 6–11 setae in each hypostomial row, rows rather divergent posteriorly from lateral margins of hypostomium. Head with extent and intensity of pigmentation varied, head-spots very indefinite but areas where spots normally occur generally paler than surrounding areas, pattern apparently therefore essentially negative. Postgenal cleft large, very much longer than postgenal bridge, subtriangular with rounded tip or broadly sagittate and sharply pointed anteriorly. Mandible normal, first comb-tooth very large and subequal to one of the outer apical teeth, second and third comb-teeth small and short and subequal or second shorter than third, second and third comb-teeth very much shorter than and strikingly differentiated from succeeding long fine comb-teeth ; two mandibular serrations. Antenna of medium length (slightly longer than stem of cephalic fan), with four segments, occasionally appearing to have fifth segment through differential pigmentation of second segment. Thoracic cuticle bare. Abdomen widening gradually to sixth and seventh segments, widest well before circler. Abdominal cuticle bare. Ventral papillae absent. Accessory sclerites absent. Rectal scales present. Rectal gills usually without secondary lobules, rarely a few thumb-like secondaries near base of each main lobe. Posterior circler with 70–100 rows of 11–19 hooks.

**Distribution.** Southern parts of the Palaearctic Region, from Spain through Mediterranean Europe to Transcaucasia, Soviet Central Asia, Afghanistan, Kashmir, Tibet and Sinkiang ; also North Africa (Morocco and Algeria : Map 11).

**Discussion.** The small subgenus *Tetisimulium* is a distinctive group in the *Simulium* s.l. fauna of the drier, most southerly, areas of the Palaearctic mainland, the females being very easily recognized by the pale greyish pollinose scutum with its three broad dark longitudinal lines (pattern usually much as in Text-fig. 73) and by the pale grey abdomen with three lines of large dark spots. The large abdominal tergites 6–8 of the female, which in the subgenera *Simulium* s. str. and *Odagmia* are rather shining polished black or black-brown, are entirely pollinose in *Tetisimulium* females and usually pale grey with or without a darker median line, and the abdom-

inal pattern and pollinosity forms a useful distinguishing feature for the subgenus (in addition to those mentioned below).

The male hypopygium in *Tetisimulium* is of the same type as that in *Odagmia* and *Simulium* s. str., having a generally similar form of ventral plate to that found in *Odagmia* (although lacking such a definite beak-like process as in this subgenus), and having similar long heavy styles, similar median sclerite and the same form of paramere and parameral hooks, and there seems no doubt that *Tetisimulium* is closely related to both *Odagmia* and *Simulium* s. str. The pupal characters are essentially the same as in these subgenera, and the fenestrate cocoon is like that of many forms of *Simulium* s. str. (including *Gnus*), although it may be noted that *Tetisimulium* pupae normally only have a dorsal spine-comb on the eighth abdominal tergum, whereas pupae of these other subgenera most often have spine-combs on some adjacent segments in addition. The larval stage in *Tetisimulium* is closely similar to that of *Simulium* s. str., with bare cuticle, large pointed and broadly sagittate or subcordate postgenal cleft, and with an indefinitely pigmented head in which it is difficult to classify the pattern as being either positive or negative (though probably a basic negative pattern since the areas of the spots are normally paler than other parts of the head capsule). All three subgenera *Tetisimulium*, *Odagmia* and *Simulium* s. str. agree in having the female cibarium minutely toothed between the cornuae.

Apart from the female pattern already discussed, *Tetisimulium* differs from *Odagmia* and *Simulium* s. str. by having a very slender fore tarsus (Text-fig. 85) in both sexes, and differs from *Simulium* s. str. (but not from *Odagmia*) in having the pleural membrane haired. The larva has a much larger and more pointed postgenal cleft than that of *Odagmia* larvae, and has no definite ventral papillae (small bluntly rounded papillae are usually distinguishable in *Odagmia*); there appears to be no satisfactory character separating larvae of *Tetisimulium* from those of *Simulium* s. str. but the first mandibular comb-tooth seems usually to be much larger, and the second and third comb-teeth relatively much smaller, in *Tetisimulium* larvae.

The Nearctic subgenera *Hagenomyia* Shewell (see Introduction) and *Psilozia* Enderlein (of which the latter occurs in Greenland and Iceland as well as North America) have a strong resemblance to the Palaearctic *Tetisimulium* and may be rather closely related to it, more especially *Hagenomyia*: the females of all three subgenera are very similar because of the contrasting pale grey and blackish patterned scutum and abdomen, and (like *Tetisimulium*) females of both *Hagenomyia* and *Psilozia* differ from *Simulium* s. str. (including *Gnus*) and *Odagmia* by having the large abdominal tergites 6-8 grey pollinose instead of shining blackish. The scutal pattern in the females of *Hagenomyia* and *Psilozia*, however, includes a blackish brown lyre-shaped mark in addition to the three broad brownish vittae such as occur in *Tetisimulium* (these, though found in *Hagenomyia* and *Psilozia*, are less conspicuous in these subgenera and it is the narrower blackish lines of the lyre-shaped mark that stand out). Both *Hagenomyia* and *Psilozia* have the pleural membrane bare and differ in this respect from *Tetisimulium*, and the ventral plate of the males is of very different shape, but the three subgenera agree in having the fore

tarsi slender and the base of the radius bare. *Tetisimulium* resembles *Hagenomyia* in having a well developed and rather hairy seventh sternite in the female and in the elongate styles of the male hypopygium, in the shape of the larval postgenal cleft, and to a lesser extent in the form of the cocoon and pupal gill (although in *Hagenomyia* gill there are nine filaments and not six or eight), but it differs by having the cibarium toothed (unarmed in *Hagenomyia*) and in the form of the larval mandibular comb-teeth (all very large in *Hagenomyia*); it resembles *Psilozia* in having the cibarium toothed, in the simple larval rectal gills and in the shape of the female gonapophyses (slightly produced but rounded), but differs from *Psilozia* in the long styles with single spinule (in *Psilozia* the male styles are short and subquadrate with 2-4 apical spinules), in the larger pointed larval postgenal cleft, in the differently formed larval mandibular comb-teeth and in cocoon and pupal gill form.

The Palaearctic subgenus *Obuchovia* Rubzov has an almost identical distribution to that of *Tetisimulium*, being largely confined to the more arid parts of the region and particularly characteristic of the black-fly fauna of Soviet Central Asia: but *Obuchovia* is not known from North Africa, and probably does not occur there. *Obuchovia* has a superficial resemblance to *Tetisimulium* because of its haired pleural membrane, bare base to the radius, often slender fore tarsi, almost simple female claws, patterned female abdomen, and elongate heavy male styles, but there is almost certainly little if any close relationship: in *Obuchovia* the male ventral plate is flat and rounded, the pupal gill very short and concealed within the closely woven long-necked cocoon, there are no dorsal spine-combs on any of the terminal pupal abdominal segments, the form of the larval abdomen, mandibular comb-teeth and hypostomium are quite different, the female gonapophyses are elongate tongue-like and the cibarium is unarmed.

The species of *Tetisimulium* form a homogeneous subgenus, and no species-groups are recognized.

Included taxa. All taxa placed in *Tetisimulium* by Rubzov (1959-1964), of which only one species occurs in North Africa (Morocco and Algeria): *Simulium* (*Tetisimulium*) *bezzii* (Corti).

[Note: the publication date for *Melusina bezzii* Corti has always been cited erroneously in the taxonomic literature as 1916, but the name *bezzii* is nomenclaturally available from its earlier citation in the key given by Corti (1914: 197, 198), and the correct date for the species is 1914. *Simulium atlas* Séguy, described from Morocco by Séguy (1930), is a synonym of *bezzii*: synonymy established by Grenier & Theodorides (1953: 439)].

#### Subgenus **ODAGMIA** Enderlein

*Odagmia* Enderlein, 1921: 199. Type-species: *Simulia ornata* Meigen, 1818, by original designation.

*Discosphyria* Enderlein, 1922: 72. Type-species: *Discosphyria odagmiina* Enderlein, 1922, by original designation.

Diagnosis. ♂♀: Basal section of radius bare. Pleural membrane haired. Katepisternum

bare. Fore tarsus dilated, fore basitarsus 4-6 times as long as its greatest breadth. ♀: cibarium armed with some very minute denticles. Tarsal claws with very small basal tooth. Scutum with boldly marked pale grey pattern anteriorly, the grey mark more or less anchor-shaped or as a pair of horse-shoes meeting in mid-line and with open ends directed outwards. Abdomen sparsely fine haired, sixth to eighth tergites shining and preceding tergites matt. Seventh sternite undeveloped. Gonapophyses simple bluntly rounded lobes, occasionally slightly obtuse-angulate at the tips. Paraprocts normal. Spermatheca without reticulate surface pattern or internal hairs. ♂: scutum with a pair of bright silvery shoulder patches. Genitalia with very large elongate subparallel-sided styles which are about two or three times as long as the coxites, style with a single apical spinule; coxite not produced beyond base of style; ventral plate complex, body of plate narrow and heavily toothed apically, with a coarsely haired ventral or anteroventral process (usually forming a broad tapering projection in profile), basal arms widely divergent; median sclerite large and subovate, deeply cleft apically and with edges serrate or frayed at posterior end; parameres broad basally but strongly tapering towards parameral hooks, usually subtriangular, parameral hooks very numerous. *Pupa*: Gill with 8 simple elongate filaments arising near base, nearly always in four regular pairs each with a short common stem; gill filaments spreading basally but bending so that tips are approximated, directed for wards and extending far beyond cocoon; gill about as long as pupal body. Abdominal onchotaxy normal; segments 7 and 8, and usually also segment 6, dorsally with spine-combs. Cocoon simple, anterior margin usually a little thickened, without anterodorsal median projection, slipper-shaped, loosely woven but not fenestrate. *Larva*: Head and cephalic fans normal. Hypostomium with usual nine apical teeth, these blunt or only slightly prominent; 4-10 setae in each hypostomial row, rows subparallel to or slightly divergent posteriorly from lateral margins of hypostomium. Head-spots positive, boldly marked and usually not obscured by infuscation of surrounding areas. Postgenal cleft small, shorter than postgenal bridge or about equal in length to it, subquadrate or evenly rounded. Mandible normal, first three comb-teeth evenly decreasing in size, other comb-teeth very long and fine and sharply differentiated from first three; two mandibular serrations. Antenna of medium length, with four segments (rarely an apparent fifth because of secondary annulation). Thoracic cuticle bare. Abdomen broadest at sixth or seventh segment, well before posterior circlet. Abdominal cuticle bare. Ventral papillae present but small, bluntly rounded and inconspicuous. Accessory sclerites absent. Rectal scales present. Rectal gills usually without secondary lobules, sometimes from one to four small secondaries on each lobe. Posterior circlet with 60-110 rows of 12-15 hooks.

**Distribution.** An entirely Palaearctic subgenus found throughout most of the region, the distribution including Madeira, Canary Islands and North Africa (Map 11). Present in Japan, absent from Iceland.

**Discussion.** The subgenus *Odagmia* as here restricted is equivalent only to the *ornatum*-group of *Odagmia* as treated by Rubzov (1959-1964) in his monograph of Palaearctic Simuliidae, and the *variegatum*-group (included in *Odagmia* by Rubzov) is excluded, since it has the pleural membrane bare and has other characters that on balance place it in *Simulium* s. str. much more satisfactorily than in *Odagmia*. Davies (1966: 421) has adduced arguments for not recognizing *Odagmia* as a valid subgenus, and places the type-species *Simulium ornatum* Meigen in the subgenus *Simulium* s. str., thus treating *Odagmia* as a synonym of *Simulium* in the restricted sense; in the present work, as in my paper on the Simuliidae of the Middle East (Crosskey, 1967b), it is preferred—while recognizing the undoubted close relationship between the subgenera—to accept *Odagmia* as a valid subgenus. As here treated it includes *ornatum* and all its immediate allies that differ consistently from *Simulium* s. str. by having the pleural membrane haired; in addition they differ from many

but not all forms of *Simulium* s. str. by the constant possession of a small spinule-like tooth at the base of the female claw, by the presence of eight gill filaments that almost always branch in regular pairs, by the non-fenestrate cocoon, and by the much smaller postgenal cleft and usually simple rectal gills of the larva. These same characters distinguish *Odagmia* from *Gnus* Rubzov, a name that Rubzov and Stone apply to a genus-group segregate that they consider distinct from *Simulium* s. str. but which is here treated as a synonym of the latter (for further discussion of the status of *Gnus* see under *Simulium* s. str. below).

The *Odagmia* segregate is not represented in the *Simulium* fauna of the New World and does not, in the Old World, extend into the Oriental Region : Puri (1932a) saw two specimens with haired pleural membrane, identified by him as *ornatum* Meigen, supposedly collected at Cannanore in South India, but considered that there must have been an error of labelling (this is probably true, as later collections of Simuliidae from the Oriental Region have not revealed the presence of *ornatum*-like forms in the area). In the Mediterranean area, including the Canary Islands, Morocco, and the Middle East, species of *Odagmia* form a main component of the *Simulium* s.l. fauna, and in many parts are the only species present in the fauna in which the adults have the basal section of the radius bare (most of the black-fly communities of the southern Mediterranean areas are comprised by forms of the subgenera *Eusimulium* and *Wilhelmia* in which the adults have the radius entirely haired).

The Canary Islands are the type-locality of three supposed species belonging in subgenus *Odagmia*, viz. *S.(O.) intermedium* Roubaud, 1906 ; *S.(O.) H-nigrum* (Santos Abreu, 1922) ; and *S.(O.) insolitum* (Santos Abreu, 1922). No immature stages of any Simuliidae have yet been collected in the Canary Islands and this makes it difficult to recognize the specific identity of forms described from there with any reliability, but it appears almost certain that some or all of these names are synonymous either with *S.(O.) ornatum* Meigen or *S.(O.) nitidifrons* Edwards, which occur widely in western Europe and (*nitidifrons* particularly) in North Africa from Morocco to Tunisia : *insolitum*, *H-nigrum*, and *intermedium* from the Canaries are all based on unique female holotypes that have the frons semi-shining (as in *nitidifrons*) and the legs rather extensively pale, and appear to be conspecific with each other and also with shining-frons forms of *Odagmia* from the North African mainland identified in the literature as *nitidifrons* (Edwards, 1923 ; Grenier, 1953 ; Grenier & Theodorides, 1953 ; Grenier, Faure & Laurent, 1957). *Simulium egregium* Séguy, 1930, based on a female holotype from Morocco, is probably also the same, but no re-examination of the type has been made since the original description.

Finally, it may be useful to enumerate the main characteristics that *Odagmia* shares with *Simulium* s. str. ; basal section of radius bare, fore tarsus dilated, katepisternum bare, minute denticles or nodules on cibarium between cornuae, similar adult abdomen in both sexes, same form of male hypopygium with heavy elongate styles and complex toothed ventral plate, filamentous pupal gill, similar larval mandibles and larval body shape, bare larval cuticle.

Included taxa. All forms with haired pleural membrane forming the *ornatum*-

group of *Odagmia* in Rubzov (1959-1964 : 457-480). Also taxa from Canary Islands omitted by Rubzov and listed below, together with *S.(O.) spinosum* Doby & Deblock from western Europe and the few recently described forms of the *ornatum*-group not included in Rubzov's coverage. Also *S.(O.) odagmiinum* (Enderlein). The included taxa from the African area are :

Canary Islands : *Simulium (Odagmia) intermedium* Roubaud ; *S.(O.) insolitum* (Santos Abreu) ; *S.(O.) H-nigrum* (Santos Abreu). [Note : all three of these names probably synonymous.]

North Africa : *Simulium (Odagmia) nitidifrons* Edwards ; *S.(O.) ornatum* Meigen ; *S.(O.) egregium* Séguy. [Note : the species from North Africa identified by authors as *nitidifrons* is probably the same as *intermedium* Roubaud, but establishment of definite synonymy is not possible at this time.]

### Subgenus *SIMULIUM* Latreille s. str.

*Simulium* Latreille, 1802 : 426. Type-species : *Rhagio colombaschensis* Fabricius, 1787, by monotypy.

*Gynonychodon* Enderlein, 1925 : 208. Type-species : *Simulium nobile* de Meijere, 1907, by original designation.

*Pseudodagmia* Baranov, 1926 : 164. Type-species : *Simulia variegata* Meigen, 1818, by original designation. (As subgenus of *Simulium* Latreille, 1802.)

*Pseudosimulium* Baranov, 1926 : 164. Type-species : *Simulia argyreata* Meigen, 1838, by original designation. (As subgenus of *Simulium* Latreille, 1802.) Junior homonym, pre-occupied by *Pseudosimulium* Handlirsch, 1908 (Diptera).

*Aspathia* Enderlein, 1935 : 359. Type-species : *Simulium hunteri* Malloch, 1914, by original designation.

*Danubiosimulium* Baranov, 1935 : 158. Type-species : *Culex columbaczensis* Schönbauer, 1795 [= *Rhagio colombaschensis* Fabricius, 1787], by monotypy. (As subgenus of *Simulium* Latreille, 1802.)

*Cleitosimulium* Séguy & Dorier, 1936 : 141. Type-species : *Simulium rupicolum* Séguy & Dorier, 1936, by original designation. (As subgenus of *Simulium* Latreille, 1802.)

*Gnus* Rubzov, 1940 : 363. Type-species : *Simulium decimatum* Dorogostajskij, Rubzov & Vlasenko, 1935, by original designation. [Available with date 1940, since *Gnus* Rubzov, 1937 : 1290 is an unavailable *nomen nudum*.]

Diagnosis. ♂♀ : Basal section of radius bare (rarely haired in ♀). Pleural membrane bare. Katepisternum bare. Fore tarsus moderately to strongly dilated, fore basitarsus 4-6 times as long as its greatest breadth. ♀ : cibarium armed with blunt denticles or nodular granulations between cornuae, rarely apparently unarmed. Tarsal claws simple or with minute basal tooth. Scutum sometimes semi-shining without pattern, usually with definite pattern at least of grey shoulder-marks, sometimes with bold striate black and grey pattern. Abdomen shining and with sparse fine hair on broad tergites 6-8, narrower preceding tergites dull and matt, no scale covering. Seventh sternite undeveloped. Gonapophyses simple bluntly truncate or rounded lobes. Paraprocts normal. Spermatheca with or without definite polygonal pattern, without internal hairs. ♂ : scutum patterned, at least with silver or greyish shoulder-marks, often with bold black median area sharply contrasting with silver-grey pruinose margins, form of pattern varied. Genitalia with very heavy elongate subparallel-sided styles from one and a half to three times as long as the coxites, style with one apical spinule and often with an inner basal projection ; coxite not produced beyond base of style ; ventral plate complex, angled and three-dimensional, body of plate relatively small, often toothed and with haired beak-like process,

when subtriangular with divergent basal arms, but plate sometimes wider and the basal arms subparallel; median sclerite large and elongate-ovate or sometimes subcordate or subtriangular or clove-shaped, cleft apically; parameres large and broad, irregularly subtriangular, tapering towards parameral hooks, the parameral hooks very numerous. *Pupa*: Gill filamentous, branches elongate and slender (rarely rather dilated basally), filaments branching near base and numbering 6–32 at extremes of range (but filaments only in even numbers 6, 8, 10, 12, 16, 28–32, and most often 6 or 8); gill branches directed forwards but whole gill shorter than pupal body. Abdominal onchotaxy normal, segment 2 often with four small spinous supernumerary hairs or hooklets on each side dorsally, and segment 4 often with a small supernumerary hooklet each side ventrally; spine-comb present dorsally on at least segment 8 and often on other segments from 6–9 in addition. Cocoon of varied form, a simple pocket or with neck, well woven, often fenestrate anteriorly or with an open lattice formed of strong loop-like strands and large open spaces, sometimes with large wing-like lateral anterior flaps or with a large anterodorsal flap, always more or less covering pupal body. *Larva*: Head and cephalic fans normal. Hypostomium with usual nine apical teeth, teeth rather blunt and median and corner teeth not very strongly prominent; 4–15 setae in each hypostomial row, rows lying subparallel to, or only slightly divergent from, lateral margins of hypostomium. Head pigmentation varied, most often with basic negative pattern of pale spots surrounded by darker areas, the pigmentation on cephalic apotome often forming H-shaped mark, sometimes head-spots clearly positive, sometimes head with dark infuscation and spots not clearly either positive or negative. Postgenal cleft large, longer than postgenal bridge, mitre-shaped, elongate-subcordate or subtriangular, often with an anteromedian extension that meets the base of the hypostomium so that the postgenal bridge is incomplete medially. Mandible normal, first three comb-teeth evenly decreasing in size, other comb-teeth long and fine; two mandibular serrations (very rare exceptions have one or two supernumerary serrations). Antenna long or moderately long (normally longer than stem of cephalic fan), with four segments. Thoracic cuticle bare. Abdomen broadest at sixth or seventh segment, well before posterior circler. Abdominal cuticle bare. Ventral papillae absent (sides of last abdominal segment sometimes slightly swollen like rudimentary sublateral papillae). Accessory sclerites absent. Rectal scales present. Rectal gills with secondary lobules. Posterior circler with 60–160 rows of 8–25 hooks.

**Distribution.** Widely distributed throughout the Nearctic Region (including Alaska and Greenland), the Palaearctic Region (including North Africa, Japan, Sakhalin and the Kurile Islands) and the Oriental Region (including Formosa and the Ryukyu Islands). Absent from the Ethiopian, Malagasy and Australasian Regions. Probably absent from most of the Neotropical Region, but some forms from Central America have been assigned to the subgenus (Dalmat, 1955; Vargas & Diaz Najera, 1957) although atypical in several characters. In the Oriental Region distribution extends south-eastwards as far as Malaysia, western Indonesia and Philippine Republic (but not into New Guinea).

**Discussion.** In numbers of included species the subgenus *Simulium* sensu stricto (including the segregate *Gnus* Rubzov which is here considered to be a synonym) is the second largest subgeneric segregate in the *Simulium* s.l. fauna of the Holarctic Regions, including about 30 per cent. of the species in both North America and Eurasia; no recent revision exists for the Oriental Region but *Simulium* s. str. species probably account for about half the black-fly fauna of that area. The subgenus is usually looked upon, probably justifiably, as including the most 'advanced' black-flies, or at least the ones retaining the fewest generalized or 'primitive' characters, and is usually placed last in any sequential classification of

the Simuliidae (e.g. by Rubzov, 1959-1964 ; Stone, 1965 ; Davies, 1966) ; the same course is followed in the present work. The main reasons for this are the presence in *Simulium* s. str. of some adult characters that are never found in Prosimuliine forms, viz. bare basal section to the radius, enlarged and flattened fore tarsus, exceptionally enlarged and elongate styles of the male hypopygium, complex toothed and beaked ventral plate, and the boldly marked scutal pattern (though some or most of these characters are found in some other subgenera that are probably quite nearly related to *Simulium* s. str.).

The subgenus most nearly related to *Simulium* s. str. is clearly *Odagmia*, which differs by having the pleural membrane haired (always bare in *Simulium* s. str.), by the presence of a small claw-tooth in the female (claws nearly always simple in *Simulium*), by the presence of blunt ventral papillae and undivided rectal gill lobes (although exceptions to the latter do occur in *Odagmia*), and by the small rounded or quadrate larval postgenal cleft (the cleft much larger and differently shaped in the larvae of *Simulium* s. str.). These differences are not great, and it would not be inappropriate to rank *Odagmia* as merely a species-group within *Simulium* s. str. (the course recently adopted by Davies, 1966, in dealing with the British fauna, where the *ornatum*-group is placed in *Simulium* s. str.), but I prefer—because they are readily and consistently distinguishable in both adult and larval stages—to recognize both *Odagmia* and *Simulium* as valid subgenera : this course has the advantage of making *Simulium* s. str. more clearly definable than it would become if *Odagmia* was merged with it.

The same cannot be said of *Gnus*, which Rubzov (1959-1964) and Stone (1963, 1965) treat as a valid genus-group segregate distinct from *Simulium* s. str., mainly because of the presence in the claws of the female of a small basal tooth, and the loose open weave of the fore part of the cocoon, together with the long postgenal cleft of the larva that meets or almost meets the hypostomium. Neither these nor any other characters of the species that have been placed in *Gnus*, either from the North American or from the Palaearctic fauna, offer sufficiently consistent differences from the characters found in *Simulium* s. str. to justify the treatment of *Gnus* as a separate subgenus and I here unhesitatingly place *Gnus* as a synonym of *Simulium* s. str. When all forms of *Simulium* and *Gnus* are considered from the Holarctic and Oriental Regions it is at once clear that many intermediate conditions exist for any character (e.g. between the cocoon with very large openings, smaller fenestrations and no fenestrations ; between a completely simple female claw and one with a definite small tooth ; between a larval postgenal cleft that stops well short of the hypostomium and one that reaches it widely and completely divides the postgenal bridge) and that no combination of characters from different stages of development is maintained throughout any given series of species with enough constancy to enable any separate subgenus to be defined—and it is difficult to define species-groups within *Simulium* s. str. reliably.

If *Gnus* and *Simulium* s. str. are maintained as separate subgenera it becomes impossible satisfactorily to assign many species either one way or the other. As examples of this difficulty may be cited the following : *Simulium nobile* de Meijere

from Java has the incomplete larval postgenal bridge of *Gnus* but a non-fenestrate cocoon, while *S. eximium* de Meijere from Java has the usual shorter postgenal cleft and complete bridge of *Simulium* in the larva, but the front of the cocoon is widely open with loop-like strands as in *Gnus*; *S. gaudi* Grenier & Faure from Morocco has the typical cocoon of *Gnus* but a simple female claw and short postgenal cleft as in typical *Simulium*, whereas *S. degrangei* Dorier & Grenier has the larva with incomplete postgenal bridge as *Gnus* but cocoon and female claw as *Simulium*. These are but a few instances among many similar that force me to conclude that *Gnus* cannot be maintained as a valid subgenus, and that the name must be relegated to the synonymy of *Simulium* s. str.

Several other names are synonyms of *Simulium* in the restricted sense and attention must be briefly drawn to these:

*Simulium nobile* de Meijere, of which the male holotype (in Zoölogisch Museum, Amsterdam) and other material of all stages have been examined, has all the characters of *Simulium* s. str., and the generic name *Gynonychodon* Enderlein (for which *nobile* is the type-species) therefore falls in synonymy.

The *variegatum*-group, which Rubzov (1959-1964: 480) includes in *Odagmia*, has the pleural membrane bare and the larval postgenal cleft large and helmet-shaped, and does not fit into *Odagmia* as this subgenus is defined in the present work; instead I place it in *Simulium* s. str., and the genus-group name *Pseudodagmia* Baranov (of which *variegatum* Meigen is type-species) therefore falls as a synonym of *Simulium* s. str. and not of *Odagmia*. It may be remarked at this point that the *monticola*-group (which Rubzov, op. cit.: 487, also places in *Odagmia*) has the pleural membrane bare and all other essential characters of *Simulium* s. str., and this group too I assign to *Simulium*: no genus-group name is however based on any species of this group.

*Simulium argyreatum* Meigen and *Simulium rupicolum* Séguy & Dorier from Europe, and *S. hunteri* Malloch from North America, all have the characters of *Simulium* s. str. and the genus-group names based upon these type-species, viz. *Pseudosimulium* Baranov, *Cleitosimulium* Séguy & Dorier, and *Aspathia* Enderlein respectively are all synonyms of *Simulium* in the strict sense. No type-material now exists for objective comparison of either *Rhagio colombaschensis* Fabricius (type-species of *Simulium*) or of *Culex columbacensis* Schönbauer (type-species of *Danubiosimulium* Baranov), but since both names apply to the infamous Golubatz fly that is responsible for the great black-fly outbreaks of the Danube valley there is no doubt that the specific names are synonyms, and therefore that *Danubiosimulium* is an isogenotypic synonym of *Simulium* Latreille.

Stone (1963) placed the names *Psilocnetha* Enderlein and *Pselaphochir* Enderlein as synonyms of *Simulium* s. str., but it is now clear that these names apply to quite other segregates of *Simulium* s.l. and are not synonyms of *Simulium* in the restricted sense: *Psilocnetha* Enderlein is a synonym of *Byssodon* Enderlein and *Pselaphochir* is a junior synonym of *Morops* Enderlein, an endemic Australasian subgenus allied to *Eusimulium* (for diagnosis and discussion of *Morops* see Crosskey, 1967a), and there is no doubt about the segregates to which the names *Psilocnetha* and *Pselapho-*

*chir* pertain. On the other hand, the correct application of the names *Psaroniocompsa* Enderlein and *Pliodasina* Enderlein, which Stone (1963) also treats in synonymy with *Simulium* s. str., is at present very doubtful because of inadequate knowledge of the two Neotropical type-species: however, it seems certain that few if any of the many South American species of *Simulium* s.l. can legitimately be assigned to *Simulium* in the strict subgeneric sense and I therefore omit the names *Psaroniocompsa* and *Pliodasina* from the synonymy of *Simulium* s. str. until their status becomes clear.

Davies (1966 : 421) has recently given reasons for not accepting the segregate *Boophthora* Enderlein (type-species *Simulium erythrocephalum* (De Geer) = *Simulium argyreatum* of Enderlein, not of Meigen, by misidentification) as a valid subgenus and has included its type-species in *Simulium* s. str., and in an earlier paper (Crosskey, 1967*b*) I have also treated *Boophthora* as synonymous with *Simulium* s. str. However, it now appears to me after evaluation of the segregates of *Simulium* s.l. on a world basis, rather than with the narrower purview of the Palaearctic Region alone, that *Boophthora* should be accepted as a separate subgenus (in accordance with the view already expressed by Stone, 1963 : 3). The characters for distinguishing *Boophthora* and *Simulium* s. str. lie mainly, as Davies points out, in the male hypopygium (with its remarkable very short styles bearing multiple spinules in *Boophthora* as compared to the enormously long heavy styles with single apical spinule in *Simulium*), but other characters also provide distinguishing features for adults and larvae (there is no fully satisfactory character for separating pupae of *Boophthora* from those of all *Simulium* s. str. on a subgeneric basis); the larval abdomen in *Boophthora* has a pair of distinct flap-like papillae on the last segment in a lateroventral position, and the upper mesopleural region in front of the pleural membrane (sometimes also the upper part of the membrane itself) is haired.

In all the many Holarctic species of the subgenus *Simulium* s. str. the basal section of the radius is bare in both sexes, and Rubzov (1959–1964 : 509) cites the character in his diagnosis ('♂ und ♀ : Die Ader  $r_1$  ist nackt in der Basalhälfte'), but in some Oriental species of *Simulium* s. str. the basal part of the radius is haired in the female even though bare in the male as normal. Such sexual dimorphism is of such very rare occurrence in the Simuliidae that erroneous association of males and females was at first suspected, and there is still doubt about the validity of Edwards' (1934 : 104) statement that males have the radial base bare in species of his Group I, Sub-group A yet the females have it hairy: but Puri's (1932*b*) record of such dimorphism in *S.(S.) griseescens* Brunetti was based on a series of reared adults which were almost certainly correctly associated. So while it is nearly always the case that the basal section of the radius is bare in *Simulium* s. str., exceptions have to be admitted into the subgenus on totality of characters even though the base of the radius is haired and in one sex only. A comparable situation exists in the Neotropical subgenus *Psilopelmia* Enderlein in which some species have the basal section of the radius haired and others bare, and in at least one species of which (*Simulium (Psilopelmia) downsi* Vargas, Martinez Palacios & Diaz Najera) there is sexual dimorphism in the character.

The subgenus *Simulium* s. str. is probably divisible into a number of species-groups distinguishable by the number of pupal gill filaments, form of the cocoon, scutal pattern, presence or absence of a small basal tooth in the female claw and other characters, and Rubzov (1959–1964) in fact recognizes eight species-groups in the Palaearctic fauna. Only one (or possibly two) species of *Simulium* s. str. occur in Africa (Morocco and Algeria), and a consideration of species groupings within the subgenus is outside the scope of the present paper : it is hoped at some future time to review the Oriental Simuliidae, amongst which the subgenus *Simulium* forms the main faunal component, and an elucidation of the groups into which the species fall will then be relevant.

Included taxa. The subgenus includes the following forms from the Regions indicated :—

Palaearctic Region : all species-group taxa assigned to *Simulium* Latreille and *Gnus* Rubzov in Rubzov's (1959–1964) monograph, and all species-group taxa except the *ornatum*-group assigned to *Odagmia* Enderlein by Rubzov (op. cit.). From the African area only one confirmed species : *Simulium* (*Simulium*) *gaudi* Grenier & Faure (Morocco). In addition there are old records based on adults of *Simulium* s. str. species from North Africa by Séguy (1930) for *reptans* L. and *subornatum* Edwards, and from the Canary Islands by Santos Abreu (1922) for *reptans* L., *variegatum* Meigen, *cincta* Meigen, and *cinerea* Macquart but there is scarcely any doubt that these are all misidentifications.

Nearctic Region : all species assigned to *Simulium* Latreille s. str. and *Gnus* Rubzov by Stone (1965).

Oriental Region : no comprehensive work exists to which reference can be made, but the British Museum (Natural History) contains material of almost all described Oriental species, and the following are here assigned to *Simulium* s. str. after examination of types and other material in that collection : *Simulium* (*Simulium*) *aeneifacies* Edwards ; *S.*(*S.*) *argentipes* Edwards ; *S.*(*S.*) *argyrocinctum* de Meijere ; *S.*(*S.*) *baltazarae* Delfinado ; *S.*(*S.*) *barraudi* Puri ; *S.*(*S.*) *christophersi* Puri ; *S.*(*S.*) *consimile* Puri ; *S.*(*S.*) *crassimanum* Edwards ; *S.*(*S.*) *dentatum* Puri ; *S.*(*S.*) *digitatum* Puri ; *S.*(*S.*) *eximium* de Meijere ; *S.*(*S.*) *fenestratum* Edwards ; *S.*(*S.*) *fuscopilosum* Edwards ; *S.*(*S.*) *gravelyi* Puri ; *S.*(*S.*) *grisescens* Brunetti ; *S.*(*S.*) *gurneyae* Senior White ; *S.*(*S.*) *hackeri* Edwards ; *S.*(*S.*) *himalayense* Puri ; *S.*(*S.*) *hirtipannus* Puri ; *S.*(*S.*) *howletti* Puri ; *S.*(*S.*) *iridescens* de Meijere ; *S.*(*S.*) *laterale* Edwards ; *S.*(*S.*) *lineothorax* Puri ; *S.*(*S.*) *melanopus* Edwards ; *S.*(*S.*) *nebulicolum* Edwards ; *S.*(*S.*) *nigropilosum* Edwards ; *S.*(*S.*) *nilgircum* Puri ; *S.*(*S.*) *nitidithorax* Puri ; *S.*(*S.*) *nobile* de Meijere ; *S.*(*S.*) *novolineatum* Puri (= *lineatum* Puri, preocc.) ; *S.*(*S.*) *palmatum* Puri ; *S.*(*S.*) *palniense* Puri ; *S.*(*S.*) *ramosum* Puri ; *S.*(*S.*) *rufibasis* Brunetti ; *S.*(*S.*) *tenuitarsus* Puri ; *S.*(*S.*) *thienemanni* Edwards.

SUMMARY OF THE PROPOSED CLASSIFICATION OF THE SIMULIIDAE  
OF AFRICA AND ITS ISLANDS

The following synoptic catalogue shows all the species-group, genus-group and family-group taxa of the Simuliidae occurring in Africa and its islands. The area of coverage is the continent of Africa (Palaeartic Africa and the Ethiopian Region), southern Arabia (a constituent part of Ethiopian Region), the Malagasy Region (including Madagascar, Comoros, La Réunion, Mauritius, Rodriguez and the Seychelles), St. Helena and the Canary Islands, and the taxa are arranged in accordance with the re-classification proposed in the text.

Several names exist in the literature for supposed species described or known from the Canary Islands and North Africa, all of which are listed, but some of these will almost certainly prove to be synonymous when the southern Mediterranean Simuliid fauna is better known. Taxa occurring in North Africa (Morocco to Tunisia) or the Canary Islands but not occurring in the Ethiopian Region or the Malagasy Region are marked with an asterisk (\*).

Names that are taxonomically and nomenclaturally valid according to the proposed classification are given in bold-face type in the following list and synonyms are indented.

Family **SIMULIIDAE** Newman, 1834

Subfamily **SIMULIINAE** Newman, 1834

Tribe **PROSIMULIINI** Enderlein, 1921

Genus **PROSIMULIUM** Roubaud, 1906

Subgenus **PROSIMULIUM** Roubaud,

1906 s. str.\*

*HELODON* Enderlein, 1921

*TAENIOPTERNA* Enderlein,  
1925

*HELLICHIA* Enderlein, 1925

*MALLOCHELLA* Enderlein,  
1930

*MALLOCHIANELLA* Vargas  
& Diaz Najera, 1948

*UROSIMULIUM* Contini,  
1963

? *hirtipes* (Fries, 1824)

Subgenus **PROCNEPHIA** sgen. n.

*damarense* de Meillon & Hardy, 1951

*rhodesianum* Crosskey, 1968

*morotoense* (McCrae & Prentice,  
1965)

Subgenus **PARACNEPHIA** Rubzov, 1962

stat. n.

*brincki*-group

*brincki* (de Meillon, 1955) **comb. n.**

*muspratti*-group

*thornei* (de Meillon, 1955) **comb. n.**

*barnardi* (Gibbins, 1938) **comb. n.**

*harrisoni* (Freeman & de  
Meillon, 1953) **comb. n.**

*muspratti* (Freeman & de  
Meillon, 1953) **comb. n.**

*herero* (Enderlein, 1935)  
**comb. n.**

*turneri*-group

*turneri* (Gibbins, 1938) **comb. n.**

Tribe **SIMULIINI** Newman, 1834

Genus **METACNEPHIA** gen. n.\*

*blanci* (Grenier & Theodorides, 1953)  
**comb. n.\***

*tredecimata* (Edwards, 1920) **comb.  
n.\***

Genus **AFROSIMULIUM** gen. n.  
*gariépense* (de Meillon, 1953)  
 comb. n.

Genus **SIMULIUM** Latreille, 1802

Subgenus **BYSSODON** Enderlein, 1925  
*PSILOCNETHA* Enderlein,  
 1935 syn. n.  
*TITANOPTERYX* Enderlein,  
 1935  
*ECHINOSIMULIUM*  
 Baranov, 1938  
*GIBBINSIELLUM* Rubzov,  
 1962 syn. n.

**griseicolle-group**

*griseicolle* Becker, 1903  
*scapulatam* (Enderlein, 1935)  
*dentulatam* Wanson & Henrard, 1944  
*tridens* Freeman & de Meillon, 1953  
*bifila* Freeman & de Meillon, 1953  
*trispærae* Wanson & Henrard, 1944

Subgenus **DEXOMYIA** sgen. n.  
*atlanticum* Crosskey sp. n.

Subgenus **EUSIMULIUM** Roubaud, 1906  
*CNETHA* Enderlein, 1921  
*NEVERMANNIA* Enderlein,  
 1921  
*STILBOPLAX* Enderlein, 1921  
*FRIESIA* Enderlein, 1922  
*PSEUDONEVERMANNIA*  
 Baranov, 1926  
*CHELOCNETHA* Enderlein,  
 1936  
*CRYPTECTEMNIA*  
 Enderlein, 1936  
*MIODASIA* Enderlein, 1936

**latipes-group\***

*costatum* Friederichs, 1920\*

**ruficorne-group**

*ruficorne* Macquart, 1838  
*beckeri* Roubaud, 1906  
*annulipes* Becker, 1908  
*divergens* Pomeroy, 1922  
*diversipes* Edwards, 1923  
*duboisii* Fain, 1950  
*aureosimile* Pomeroy, 1920  
*brachium* Gibbins, 1936  
*simplex* Gibbins, 1936  
*elgonicum* Séguy, 1938

*nigritarse* Coquillett, 1902  
*caffrarica* (Enderlein, 1935)  
*buckleyi* de Meillon, 1944  
*vulcani* Fain, 1950  
*fuscicorne* Fain, 1950  
*katangae* Fain, 1951  
*loveridgei* Crosskey, 1965  
*speculiventre* Enderlein, 1914  
*starmuhneri* Grenier & Grjébine,  
 1963

**loutetense-group**

*rutherfordi* de Meillon, 1937  
*narcaeum* de Meillon, 1950  
*loutetense* Grenier & Ovazza, 1951

**aureum-group\***

*aureum* Fries, 1824\*  
*guimari* Becker, 1908\*  
*latinum* (Rubzov, 1962)\*  
*nigripes* (Santos Abreu, 1922)\*  
*pseudolatipes* (Santos Abreu, 1922)\*  
*submorsitans* Séguy, 1921\*  
*velutinum* (Santos Abreu, 1922)\*

Subgenus **POMEROYELLUM** Rubzov,  
 1962

**bequaerti-group**

*bequaerti* Gibbins, 1936  
*phoroniformis* de Meillon, 1937  
*harrisoni* Freeman & de Meillon, 1953

**alcocki-group**

*alcocki* Pomeroy, 1922  
*kenyanum* Séguy, 1938  
*henrardi* Gibbins, 1941  
*coalitum* Pomeroy, 1922  
*garmsi* nom. n.

*violaceum* Pomeroy, 1922 (pre-occupied)

*occidentale* Freeman & de Meillon,  
 1953 (preoccupied)

*djallonense* Roubaud & Grenier, 1943

*geigy* Garms & Häusermann, 1968

*weyeri* Garms & Häusermann, 1968

*hisseteum* Gibbins, 1936

*vargasi* Grenier & Rageau, 1949

*allaeri* Wanson, 1947

*johannae* Wanson, 1947

*roubaudi* Grenier & Rageau, 1949

*jadini* Fain, 1950

*akanyaruensis* Fain, 1950

*schwetzi* Wanson, 1947

*rodhaini* Fain, 1950

*ituriense* Fain, 1951

*evillense* Fain, Hallot & Bafort, 1966

- merops* de Meillon, 1950  
*gilleti* Fain & Hallot, 1964  
*tentaculum* Gibbins, 1936  
*impukane* de Meillon, 1936
- schoutedeni-group**  
*schoutedeni* Wanson, 1947  
*mcmahoni* de Meillon, 1940  
*altipartitum* Roubaud & Grenier, 1943
- cervicornutum-group**  
*rotundum* Gibbins, 1936  
*pauliani* Grenier & Doucet, 1949  
*unicornutum* Pomeroy, 1920  
*monoceros* Roubaud & Grenier, 1943  
*wolfsi* Wanson & Henrard, 1944  
*palmeri* Pomeroy, 1922  
*blacklocki* de Meillon, 1930  
*leberrei* Grenier, Germain & Mouchet, 1965  
*vangilsi* Wanson, 1947  
*cervicornutum* Pomeroy, 1920  
*aureliani* Fain, 1950
- kenyae-group**  
*kenyae* de Meillon, 1940
- Subgenus **MEILLONIELLUM** Rubzov, 1962  
*hirsutum* Pomeroy, 1922  
*dubium* Pomeroy, 1922  
*sexiens* de Meillon, 1944  
*adersi* Pomeroy, 1922  
*urundiense* Fain, 1950
- Subgenus **LEWISELLUM** sgen. n.  
*naevei* Roubaud, 1915  
*renauxi* Wanson & Lebled, 1950  
*woodi* de Meillon, 1930  
*nyasalandicum* de Meillon, 1930  
*goinyi* Lewis & Hanney, 1965  
*hightoni* Lewis, 1961  
*ovazzae* Grenier & Mouchet, 1959
- Subgenus **PHORETOMYIA** sgen. n.  
**berneri-group**  
*berneri* Freeman, 1954  
*kumboense* Grenier, Germain & Mouchet, 1965  
**lumbwanum-group**  
*lumbwanum* de Meillon, 1944  
**copleyi-group**  
*diceros* Freeman & de Meillon, 1953  
*rickenbachi* Germain, Grenier & Mouchet, 1966
- copleyi* Gibbins, 1941  
*marlieri* Grenier, 1950
- Subgenus **XENOSIMULIUM** sgen. n.  
*neireti* Roubaud, 1905  
*ambositrae* Grenier & Grjébine, 1958  
*iphias* de Meillon, 1951  
*imerinae* Roubaud, 1905
- Subgenus **ANASOLEN** Enderlein, 1930  
*octospicae* Gibbins, 1937  
*kauntzeum* Gibbins, 1938  
*masabae* Gibbins, 1934  
*rhodesiense* de Meillon, 1942  
*ngabogei* Fain, 1950  
*nili* Gibbins, 1934  
*dentulosum* Roubaud, 1915  
*gilvipes* Pomeroy, 1920  
*adolffriedericianum* (Enderlein, 1930)  
*ruwenzoriense* Gibbins, 1937  
*emfulae* de Meillon, 1937  
*voltae* Grenier, Ovazza & Valade, 1960  
*shoae* Grenier & Ovazza, 1956  
*bisnovem* Gibbins, 1938  
*edwardsi* Gibbins, 1937 [*nomen nudum*]
- Subgenus **FREEMANELLUM** sgen. n.  
*berghei* Fain, 1949  
*hessei* Gibbins, 1941  
*hirsutilateris* de Meillon, 1937  
*empopomae* de Meillon, 1937  
*debegene* de Meillon, 1934
- Subgenus **WILHELMIA** Enderlein, 1921\*  
*ariasi* Séguy, 1925\*  
*barbaricum* Séguy, 1930\*  
*canariense* Séguy, 1921\*  
*equinum* (Linnaeus, 1758)\*  
*mediterraneum* Puri, 1925\*  
*pseudequinum* Séguy, 1921\*  
*quadrifila* Grenier, Faure & Laurent, 1957\*  
*sergenti* Edwards, 1923\*
- Subgenus **METOMPHALUS** Enderlein, 1935  
**albivirgulatum-group**  
*albivirgulatum* Wanson & Henrard, 1944  
**bovis-group**

- wellmanni* Roubaud, 1906  
*magoebae* de Meillon, 1935  
*janzi* Marini de Araujo Abreu, 1961  
*arnoldi* Gibbins, 1937  
*chutteri* Lewis, 1965  
*bovis* de Meillon, 1930  
*faini* Wanson, 1947  
*fragai* Marini de Araujo Abreu, 1960
- medusaeforme-group**  
*africanum* Gibbins, 1934  
**medusaeforme** Pomeroy, 1920  
*ugandae* Gibbins, 1934  
*capensis* (Enderlein, 1935)  
*caffer* (Enderlein, 1935)  
*pseudomedusaeformis* de Meillon, 1936
- hargreavesi* Gibbins, 1934  
*elgonense* Gibbins, 1934  
*tisiphone* de Meillon, 1936  
*loangolense* Roubaud & Grenier, 1943
- letabum* de Meillon, 1935  
*zombaense* Freeman & de Meillon, 1953  
*taylori* Gibbins, 1938  
*ruandae* Fain, 1950  
*vorax* Pomeroy, 1922  
*limbatum* Enderlein, 1921  
 (preoccupied)  
*tangae* Smart, 1944  
*lepidum* de Meillon, 1935
- touffeum* Gibbins, 1937  
*futaense* Garms & Post, 1966  
*colasbelcouri* Grenier & Ovazza, 1951  
*cavum* Gibbins, 1938  
*obscurum* Gibbins, 1937 (preoccupied)  
*natalense* de Meillon, 1950
- Subgenus **EDWARDELLUM** Enderlein, 1921
- damnosum* Theobald, 1903  
*squamosum* (Enderlein, 1921)  
*cingulatum* (Enderlein, 1921)  
*latipollex* (Enderlein, 1936)  
*machadoi* Luna de Carvalho, 1962  
*vilhenai* Luna de Carvalho, 1962
- Subgenus **TETISIMULIUM** Rubzov, 1963\*  
*bezzii* (Corti, 1914)\*  
*atlas* Séguy, 1930
- Subgenus **ODAGMIA** Enderlein, 1921\*  
*DISCOSPHERIA* Enderlein, 1922  
*egregium* Séguy, 1930\*  
*H-nigrum* (Santos Abreu, 1922)\*  
*insolitum* (Santos Abreu, 1922)\*  
*intermedium* Roubaud, 1906\*  
*nitidifrons* Edwards, 1920\*  
*ornatum* Meigen, 1818\*
- Subgenus **SIMULIUM** Latreille, 1802  
 s. str.\*  
*GYNONYCHODON*  
 Enderlein, 1925  
*PSEUDODAGMIA* Baranov, 1926  
*PSEUDOSIMULIUM*  
 Baranov, 1926  
*ASPATHIA* Enderlein, 1935  
*DANUBIOSIMULIUM*  
 Baranov, 1935  
*CLEITOSIMULIUM* Séguy & Dorier, 1936  
*GNUS* Rubzov, 1940  
*gaudi* Grenier & Faure, 1956\*

Unplaced species and doubtful records :

A few clearly distinct species of *Simulium* s.l. are inadequately known and cannot be placed subgenerically. These are :

*Simulium gracilipes* Edwards, 1921 (Morocco : only ♀ holotype known).

*Simulium gyas* de Meillon, 1951 (Madagascar : immature stages known) (see p. 101).

*Simulium milloti* Grenier & Doucet, 1949 (Madagascar : female and immature stages known with characters suggesting possible assignment either to *Eusimulium* or to *Xenosimulium*).

In addition there are some old enigmatic records of certain species from Canary Islands and Morocco based on adults that were almost certainly misidentified : see Santos Abreu (1922) and Séguy (1930).

INDEX-CATALOGUE OF THE SPECIES-GROUP NAMES OF SIMULIIDAE  
FROM THE ETHIOPIAN AND MALAGASY REGIONS

The catalogue given below provides a complete alphabetical index to the species-group names of all Simuliidae occurring in the Ethiopian Region (including St. Helena) and in the Malagasy Region (including Seychelles). The list includes the names *annulipes* and *beckeri*, which although based on types from outside these regions (viz. from Canary Islands and Algeria respectively) are given because they are synonyms of *ruficorne*, the only Ethiopian species that occurs in the Palaearctic Region.

Each species-group name is cited in the original spelling and is accompanied by the following information : bibliographic reference ; genus of original assignment in parentheses ; status, sex or developmental stage of primary type(s) ; type-locality ; type-depository ; special nomenclatural information where pertinent. Nomenclaturally available names are shown in the index in bold type, and pre-occupied homonyms and other unavailable names in italic non-bold.

Type-locality information is restricted to the modern name of the country in which the exact locality occurs, or to the island or island group when appropriate ; for South Africa the name of the Province is given additionally. The former Belgian Congo and French Congo are cited as Democratic Republic of Congo and as Republic of Congo respectively (in accordance with the usage of the *Statesmen's Year-Book 1967-1968*).

The following abbreviations are used for showing the collections in which primary types are lodged :

BMNH	British Museum (Natural History), London
IMT	Instituto de Medicina Tropical, Lisbon
IP	Institut Pasteur, Paris
MD	Museu do Dundo, Dundo, Angola
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAC	Musée Royal de l'Afrique Central, Tervuren
SAIMR	South African Institute for Medical Research, Johannesburg
USNM	United States National Museum, Washington
ZMHU	Zoologisches Museum der Humboldt-Universität, Berlin
ZSM	Zoologischen Staatsinstitut und Museum, Hamburg

Lectotypes are designated under the appropriate entries in the index-catalogue for *damnosum*, *dentulosum*, *neavei*, *nyasalandicum*, *violaceum*, *wellmanni* and *woodi* of which syntypic type-material is in the British Museum.

***adersi*** Pomeroy, 1922, *Bull. ent. Res.* **12** : 459 (*Simulium*, as variety of *hirsutum* Pomeroy, 1922). Holotype ♂, TANZANIA (ZANZIBAR) : BMNH, London.

***adolffriedericianus*** Enderlein, 1930, *Arch. klassif. phylogen. Ent.* **1** : 94 (*Anasolen*). Holotype ♀, RWANDA : ZMHU, Berlin.

***africanum*** Gibbins, 1934, *Trans. R. ent. Soc. Lond.* **82** : 95 (*Simulium*). Holotype ♀, UGANDA : BMNH, London.

- akanyaruensis** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 113 (*Simulium*). Holotype ♂, RWANDA : MRAC, Tervuren.
- albiturgulatum** Wanson & Henrard, 1944, *E. Afr. med. J.* **21** : 35 (*Simulium*). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.
- alcocki** Pomeroy, 1922, *Bull. ent. Res.* **12** : 459 (*Simulium*). Holotype ♂, NIGERIA : BMNH, London (genitalia and leg fragments only, body of holotype lost).
- allaeri** Wanson, 1947, *Revue Zool. Bot. afr.* **40** : 213 (*Simulium*). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren and BMNH, London (1 ♂).
- altipartitum** Roubaud & Grenier, 1943, *Bull. Soc. Path. exot.* **36** : 304 (*Simulium*). Holotype pupa, REPUBLIC OF CONGO : IP, Paris.
- ambositrae** Grenier & Grjébine, 1958, *Bull. Soc. Path. exot.* **51** : 982 (*Simulium*). Syntypes ♂, ♀, pupae, larvae, MALAGASY REPUBLIC (MADAGASCAR) : IP, Paris.
- angolensis** Marini de Araújo Abreu, 1961, *Anais Inst. Med. trop., Lisb.* **18** : 85 (*Simulium*, as variety of *medusaeforme* Pomeroy, 1920). Syntypes ♂, ♀, pupae, ANGOLA : IMT, Lisbon. [Unavailable name under Article 15 of *International Code of Zoological Nomenclature*, 1961].
- annulipes** Becker, 1908, *Mitt. zool. Mus. Berl.* **4** : 72 (*Simulium*). Lectotype ♀, CANARY ISLANDS : ZMHU, Berlin.
- arnoldi** Gibbins, 1937, *Ann. trop. Med. Parasit.* **31** : 299 (*Simulium*). Holotype ♂, RHODESIA : BMNH, London.
- atlanticum** Crosskey, 1969, *Bull. Br. Mus. nat. Hist. (Ent.) Suppl.* **14** : 52 (*Simulium* (*Dexomyia*)). Holotype ♂ ex pupa, ST. HELENA : BMNH, London.
- aureliani** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 106 (*Simulium*). Syntypes ♂, ♀, RWANDA : MRAC, Tervuren and BMNH, London.
- aureosimile** Pomeroy, 1920, *Ann. Mag. nat. Hist. (9)* **6** : 78 (*Simulium*). Holotype ♂, CAMEROUN REPUBLIC : BMNH, London (fragments only on mount).
- barnardi** Gibbins, 1938, *Ann. trop. Med. Parasit.* **30** : 133 (*Simulium*). Holotype ♂ [slide-mounted], SOUTH AFRICA (CAPE PROVINCE) : lost (but fragments of ♂ and ♀ from type-series on slide mounts in BMNH, London).
- beckeri** Roubaud, 1906, *Bull. Mus. natn. Hist. nat., Paris* **12** : 520 (*Simulium*). Lectotype ♂, ALGERIA : ZMHU, Berlin. Lectotype designation by Crosskey, 1965, *Ann. Mag. nat. Hist. (13)* **7** (1964) : 666.
- bequaerti** Gibbins, 1936, *Ann. trop. Med. Parasit.* **30** : 133 (*Simulium*). Holotype ♂ [slide-mounted], DEMOCRATIC REPUBLIC OF CONGO (KATANGA) : lost.
- berghei** Fain, 1949, *Revue Zool. Bot. afr.* **42** : 296 (*Simulium*). Holotype ♂ [slide-mounted], DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.
- berneri** Freeman, 1954, *Ann. Mag. nat. Hist. (12)* **7** : 113 (*Simulium*). Holotype pupa [slide-mounted gill only], GHANA : BMNH, London.
- bertrandi** Luna de Carvalho, 1962, *Publçoes cult. Co. Diam. Angola*, No. 60 : 25 (*Simulium*, as form of *unicornutum* Pomeroy, 1920). [Unavailable name under Article 15 of *International Code of Zoological Nomenclature*, 1961].
- bifila** Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 137 (*Simulium*, as form of *griseicolle* Becker, 1903). Holotype ♂, SUDAN : BMNH, London.

- bisnovem** Gibbins, 1938, *Ann. trop. Med. Parasit.* **32** : 23 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- blacklocki** de Meillon, 1930, *Bull. ent. Res.* **21** : 189 (*Simulium*). Holotype ♂, SIERRA LEONE : BMNH, London.
- Authorship of the name *blacklocki* is attributable to de Meillon (1930, *Bull. ent. Res.* **21** : 189), although he cited Edwards as author in the original description : there is no evidence that Edwards was responsible for the conditions that make the name available, and authorship is by de Meillon under Article 50 of the *International Code of Zoological Nomenclature*.
- bovis** de Meillon, 1930, *Bull. ent. Res.* **21** : 188 (*Simulium*). Holotype ♀, SOUTH AFRICA (ZULULAND) : BMNH, London.
- brachium** Gibbins, 1936, *Trans. R. ent. Soc. Lond.* **85** : 230 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- brincki** de Meillon, 1955, *S. Afr. anim. Life* **2** : 348 (*Cnephia*). Holotype ♂, SOUTH AFRICA (CAPE PROVINCE) : SAIMR, Johannesburg.
- buckleyi** de Meillon, 1944, *Proc. R. ent. Soc. Lond.* (B) **13** : 118 (*Simulium*). Holotype ♂, KENYA : SAIMR, Johannesburg.
- caffer** Enderlein, 1935, *Sber. Ges. naturf. Freunde Berl.* **1935** : 362 (*Metomphalus*). Holotype ♂, SOUTH AFRICA : ZMHU, Berlin.
- caffratica** Enderlein, 1935, *Sber. Ges. naturf. Freunde Berl.* **1935** : 359 (*Cnetha*). Lectotype ♂, SOUTH AFRICA (CAPE PROVINCE) : ZMHU, Berlin. Lectotype designation by Freeman and de Meillon, 1953, *Sim. Ethiop. Reg.* : 102.
- capensis** Enderlein, 1935, *Sber. Ges. naturf. Freunde Berl.* **1935** : 361 (*Thyrsopelma*). Lectotype ♀, SOUTH AFRICA (CAPE PROVINCE) : ZMHU Berlin. Lectotype designation by Freeman and de Meillon, 1953, *Sim. Ethiop. Reg.* : 179.
- cavum** Gibbins, 1938, *Ann. trop. Med. Parasit.* **32** : 26 (*Simulium*). Replacement name for *Simulium obscurum* Gibbins, 1937, preoccupied in *Simulium* by *obscurum* Enderlein, 1924. Holotype ♂, UGANDA : BMNH, London.
- cervicornutum** Pomeroy, 1920, *Ann. Mag. nat. Hist.* (9) **6** : 73 (*Simulium*). Holotype ♂, CAMEROUN REPUBLIC : BMNH, London.
- chutteri** Lewis, 1965, *Ann. Mag. nat. Hist.* (13) **7** (1964) : 452 (*Simulium*). Holotype ♂, SOUTH AFRICA (CAPE PROVINCE) : BMNH, London.
- cingulatum** Enderlein, 1921, *Sber. Ges. naturf. Freunde Berl.* **1921** : 80. (*Edwardsellum*). Holotype ♀, SUDAN : lost.
- coalitum** Pomeroy, 1922, *Bull. ent. Res.* **12** : 460 (*Simulium*, as variety of *alcocki* Pomeroy, 1922). Holotype ♂, NIGERIA : BMNH, London.
- colasbelcouri** Grenier & Ovazza, 1951, *Bull. Soc. Path. exot.* **44** : 222 (*Simulium*). Syntypes ♂, ♀, pupae, larvae, REPUBLIC OF CONGO : IP, Paris.
- copleyi** Gibbins, 1941, *E. Afr. med. J.* **18** : 210 (*Simulium*). Holotype ♂ [slide-mounted], KENYA : lost.
- damarensis** de Meillon & Hardy, 1951, *J. ent. Soc. sth. Afr.* **14** : 30 (*Prosimulium*). Holotype ♂ [slide-mounted], SOUTH-WEST AFRICA : SAIMR, Johannesburg.
- damnosum** Theobald, 1903, *Rep. sleep. Sickn. Commn R. Soc.* **3** : 40 (*Simulium*). LECTOTYPE ♀ [by present designation], UGANDA : BMNH, London.

Existing type-material of *Simulium damnosum* consists of two conspecific female syntypes, each bearing two handwritten labels reading 'Uganda Dr. Christy' and 'Simulium damnosum (Type) F.V.T.', and both in British Museum (Natural History); the head of one syntype is missing. The syntype retaining the head has been labelled and is here designated as lectotype: the head-less syntype has been labelled as paralectotype.

**debegene** de Meillon, 1934, *Publs S. Afr. Inst. med. Res.* **6** : 253 (*Simulium*). Holotype ♀, SOUTH AFRICA (TRANSVAAL) : SAIMR, Johannesburg.

**dentulatum** Wanson & Henrard, 1944, *E. Afr. med. J.* **21** : 42 (*Simulium*, as variety of *griseicolle* Becker, 1903). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.

**dentulosum** Roubaud, 1915, *Bull. Soc. ent. Fr.*, **1915** : 294 (*Simulium*). LECTOTYPE ♀ [by present designation], UGANDA : BMNH, London.

Roubaud described *dentulosum* from seven female specimens collected by Neave and stated to be in the British Museum collection. Three of these female syntypes now exist in the collection of BMNH, London, and one with data 'Uganda Prot. Siroko R., near W. foot of Mt. Elgon. 3600 ft. Aug. 12-14, 1911. S. A. Neave' has been labelled and is here designated as lectotype.

**diceros** Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 123 (*Simulium*). Holotype ♂, DEMOCRATIC REPUBLIC OF CONGO : IP, Paris.

**divergens** Pomeroy, 1922, *Bull. ent. Res.* **12** : 460 (*Simulium*). Holotype ♂, NIGERIA : BMNH, London.

**diversipes** Edwards, 1923, *Ann. Mag. nat. Hist.* (9) **12** : 333 (*Simulium*). Holotype ♂, MAURITIUS (RODRIGUEZ ISLAND) : BMNH, London.

**djallonense** Roubaud & Grenier, 1943, *Bull. Soc. Path. exot.* **36** : 299 (*Simulium*). Syntypes ♂, pupae, GUINEA : IP, Paris.

**dubium** Pomeroy, 1922, *Bull. ent. Res.* **12** : 459 (*Simulium*, as variety of *hirsutum* Pomeroy, 1922). Lectotype ♂, TANZANIA (TANGANYIKA) : BMNH, London. Lectotype fixation as 'holotype' by Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 109.

Original material of *dubium* consists of a pupa, pupal parts, and parts of one adult female and one adult male (all syntypic material) from Morogoro, Tanganyika, mounted on five card mounts in pinned collection in British Museum (Natural History) : Freeman & de Meillon (loc. cit.) cite the single male as 'holotype', restricting the name to a single specimen and thereby providing valid fixation of a lectotype.

**duboisi** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 104 (*Simulium*). Syntypes ♂, ♀, pupae, RWANDA : MRAC, Tervuren (adults and pupae) and BMNH, London (pupae).

**duodecimum** Gibbins, 1936, *Trans. R. ent. Soc. Lond.* **85** : 223 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.

**edwardsi** Gibbins, 1937, *Bull. ent. Res.* **28** : 304 (*Simulium*). *Nomen nudum*.

**elgonensis** Gibbins, 1934, *Trans. R. ent. Soc. Lond.* **82** : 91 (*Simulium*). Holotype ♀, UGANDA : BMNH, London.

- elgonicum** Séguy, 1938, *Mem. Mus. natn. Hist. nat., Paris* (N.S.) **8** : 323. (*Simulium*). Syntypes ♂, ♀, KENYA : MNHN, Paris.
- emfulae** de Meillon, 1937, *Publs S. Afr. Inst. med. Res.* **7** : 393 (*Simulium*). Holotype ♂, SOUTH AFRICA (ZULULAND) : SAIMR, Johannesburg.
- empopomae** de Meillon, 1937, *Publs S. Afr. Inst. med. Res.* **7** : 393 (*Simulium*). Holotype ♂, SOUTH AFRICA (ZULULAND) : SAIMR, Johannesburg.
- evillense** Fain, Hallot & Bafort, 1966, *Revue Zool. Bot. afr.* **74** : 206 (*Simulium*). Holotype ♀, DEMOCRATIC REPUBLIC OF CONGO (KATANGA) : MRAC, Tervuren.
- faini** Wanson, 1947, *Revue Zool. Bot. afr.* **40** : 201 (*Simulium*). Syntypes ♂, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.
- fragai** Marini de Araújo Abreu, 1960, *Anais Inst. Med. trop., Lisb.* **17** : 698 (*Simulium*). Syntypes ♂, ♀, pupae, ANGOLA : IMT, Lisbon.
- fuscicorne** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 121 (*Simulium*, as variety of *vulcani* Fain, 1950). Syntypes ♂, pupae, RWANDA : MRAC, Tervuren and BMNH, London.
- futaense** Garms & Post, 1966, *Z. Tropenmed. Parasit.* **17** : 40 (*Simulium*). Holotype pupa, GUINEA : ZSM, Hamburg.
- garipeensis** de Meillon, 1953, *J. ent. Soc. sth. Afr.* **16** : 227 (*Simulium*). Holotype ♂, SOUTH AFRICA (ORANGE FREE STATE) : SAIMR, Johannesburg.
- garmsi nom. n.** for *occidentale* Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 56, preoccupied by *occidentale* Townsend, 1891, *Psyche, Camb.* **6** : 107. Lectotype ♂, NIGERIA : BMNH, London. (For designation see under *violaceum* Pomeroy).
- Freeman & de Meillon (1953, *Sim. Ethiop. Reg.* : 56) published the name *occidentale* as a replacement name for *violaceum* Pomeroy, 1922, a junior primary homonym in *Simulium* of *violaceum* Enderlein, 1922, but *occidentale* Freeman & de Meillon is an invalid replacement name since it is itself a junior primary homonym of *occidentale* Townsend, 1891. The new name *garmsi* is here proposed as replacement name for the preoccupied *occidentale* Freeman & de Meillon ; since both names are replacement names the lectotype of *violaceum* Pomeroy is the primary type for each (see under *violaceum*).
- geigyi** Garms & Häusermann, 1968, *Revue Zool. Bot. afr.* **78** : 66 (*Simulium*). Holotype ♂ ex pupa, TANZANIA : ZSM, Hamburg.
- gilleti** Fain & Hallot, 1964, *Revue Zool. Bot. afr.* **70** : 301 (*Simulium*). Holotype ♂ pupa, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.
- gilvipes** Pomeroy, 1920, *Ann. Mag. nat. Hist.* (9) **6** : 75 (*Simulium*). Holotype ♂, CAMEROUN REPUBLIC : BMNH, London.
- goinyi** Lewis & Hanney, 1965, *Proc. R. ent. Soc. Lond.* (B) **34** : 12 (*Simulium*). Holotype ♀, KENYA : BMNH, London.
- griseicollis** Becker, 1903, *Mitt. zool. Mus. Berl.* **2** : 78 (*Simulium*). Lectotype ♂, EGYPT : ZMHU, Berlin. Lectotype designation by Crosskey, 1965, *Ann. Mag. nat. Hist.* (13) **7** (1964) : 668.
- gyas** de Meillon, 1951, *Mém. Inst. scient. Madagascar* (A) **5** : 73 (*Simulium*). Holotype pupa, MALAGASY REPUBLIC (MADAGASCAR) : SAIMR, Johannesburg.

- hargreavesi** Gibbins, 1934, *Trans. R. ent. Soc. Lond.* **82** : 83 (*Simulium*). Holotype ♀, UGANDA : BMNH, London.
- harrisoni** Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 34 (*Cnephia*). Holotype ♂, SOUTH AFRICA (CAPE PROVINCE) : SAIMR, Johannesburg.
- harrisoni** Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 85 (*Simulium*). Holotype ♂, SOUTH AFRICA (CAPE PROVINCE) : SAIMR, Johannesburg.
- henrardi** Gibbins, 1941, *E. Afr. med. J.* **18** : 212 (*Simulium*, as variety of *alcocki* Pomeroy, 1922). Holotype pupa, DEMOCRATIC REPUBLIC OF CONGO : whereabouts not traced, probably lost.
- herero** Enderlein, 1935, *Sber. Ges. naturf. Freunde Berl.* **1935** : 358 (*Astega*). Holotype ♀, SOUTH-WEST AFRICA : ZMHU, Berlin.
- hessei** Gibbins, 1941, *E. Afr. med. J.* **18** : 211 (*Simulium*). Holotype ♂, SOUTH AFRICA (CAPE PROVINCE) : lost (five specimens with identical data to holotype in Cape Town Museum).
- hightoni** Lewis, 1961, *Proc. R. ent. Soc. Lond.* (B) **30** : 110 (*Simulium*). Holotype ♀, KENYA : BMNH, London.
- hirsutilateris** de Meillon, 1937, *Publs S. Afr. Inst. med. Res.* **7** : 395 (*Simulium*). Holotype ♂, SOUTH AFRICA (ZULULAND) : SAIMR, Johannesburg.
- hirsutum** Pomeroy, 1922, *Bull. ent. Res.* **12** : 458 (*Simulium*). Holotype ♂, TANZANIA (TANGANYIKA) : BMNH, London.
- hisseteum** Gibbins, 1936, *Ann. trop. Med. Parasit.* **30** : 138 (*Simulium*). Holotype ♂ [slide-mounted], DEMOCRATIC REPUBLIC OF CONGO : BMNH, London.
- imerinae** Roubaud, 1905, *Bull. Mus. natn. Hist. nat., Paris* **11** : 426 (*Simulium*). Syntypes ♀, MALAGASY REPUBLIC (MADAGASCAR) : MNHN, Paris.
- impukane** de Meillon, 1936, *Publs S. Afr. Inst. med. Res.* **7** : 208 (*Simulium*). Holotype ♂, SOUTH AFRICA (ZULULAND) : SAIMR, Johannesburg.
- iphias** de Meillon, 1951, *Mém. Inst. scient. Madagascar* (A) **5** : 71 (*Simulium*). Holotype ♂, MALAGASY REPUBLIC (MADAGASCAR) : SAIMR, Johannesburg.
- ituriense** Fain, 1951, *Revue Zool. Bot. afr.* **45** : 8 (*Simulium*). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren and BMNH, London.
- jadini** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 112 (*Simulium*). Holotype ♂, RWANDA : MRAC, Tervuren.
- janzi** Marini de Araújo Abreu, 1961, *Anais Inst. Med. trop., Lisb.* **18** : 83 (*Simulium*). Syntypes ♂, ♀, pupae, ANGOLA : IMT, Lisbon.
- johannae** Wanson, 1947, *Revue Zool. Bot. afr.* **40** : 210 (*Simulium*). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren and BMNH, London (1 ♂).
- katangae** Fain, 1951, *Revue Zool. Bot. afr.* **45** : 5 (*Simulium*). Holotype ♂ DEMOCRATIC REPUBLIC OF CONGO (KATANGA) : MRAC, Tervuren.
- kauntzeum** Gibbins, 1938, *Ann. trop. Med. Parasit.* **32** : 23 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- kenyae** de Meillon, 1940, *E. Afr. med. J.* **16** : 448 (*Simulium*). Holotype ♂, KENYA : SAIMR, Johannesburg.

- kenyanum** Séguy, 1938, *Mém. Mus. natn. Hist. nat., Paris* (N.S.) **8** : 325 (*Simulium*).  
Syntypes ♂, ♀, KENYA : MNHN, Paris.
- kumboense** Grenier, Germain & Mouchet, 1965, *Bull. Soc. Path. exot.* **58** : 277 (*Simulium*, as subspecies of *berneri* Freeman, 1954). Syntypes pupae and larvae, CAMEROUN REPUBLIC : IP, Paris.
- latipollex** Enderlein, 1936, *Sber. Ges. naturf. Freunde Berl.* **1936** : 127 (*Metomphalus*).  
Holotype ♀, SOUTH AFRICA (TRANSVAAL) : ZMHU, Berlin.
- leberrei** Grenier, Germain & Mouchet, 1965, *Bull. Soc. Path. exot.* **58** : 549 (*Simulium*).  
Holotype ♂, CAMEROUN REPUBLIC : IP, Paris.
- lepidum** de Meillon, 1935, *Publs S. Afr. Inst. med. Res.* **6** : 336 (*Simulium*).  
Holotype ♀, SOUTH AFRICA (TRANSVAAL) : SAIMR, Johannesburg.
- letabum** de Meillon, 1935, *Publs S. Afr. Inst. med. Res.* **6** : 330 (*Simulium*).  
Holotype ♀, SOUTH AFRICA (TRANSVAAL) : SAIMR, Johannesburg.
- limbatum** Enderlein, 1921, *Sber. Ges. naturf. Freunde Berl.* **1921** : 78 (*Simulium*).  
Lectotype ♂, TANZANIA (TANGANYIKA) : ZMHU, Berlin. Lectotype designation by Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 187.  
Name preoccupied by *Simulium limbatum* Knab, 1915 (*Bull. ent. Res.* **6** : 280), see *tangae* Smart, 1944.
- loangolense** Roubaud & Grenier, 1943, *Bull. Soc. Path. exot.* **36** : 292 (*Simulium*).  
Syntypes ♂, pupae, REPUBLIC OF CONGO, GUINEA : IP, Paris.
- loutetense** Grenier & Ovazza, 1951, *Bull. Soc. Path. exot.* **44** : 226 (*Simulium*).  
Syntypes ♂, ♀, pupae, REPUBLIC OF CONGO : IP, Paris.
- loveridgei** Crosskey, 1965, *Proc. R. ent. Soc. Lond.* (B) **34** : 33 (*Simulium* (*Eusimulium*)).  
Holotype ♂, St. HELENA : BMNH, London.
- lumbwanus** de Meillon, 1944, *Proc. R. ent. Soc. Lond.* (B) **13** : 117 (*Simulium*).  
Holotype ♂, KENYA : SAIMR, Johannesburg.
- machadoi** Luna de Carvalho, 1962, *Publçoes cult. Co. Diam. Angola*, No. 60 : 40 (*Simulium*).  
Syntypes ♂, ♀, pupae, larvae, ANGOLA : MD, Dundo and BMNH, London.
- magoebae** de Meillon, 1935, *Publs S. Afr. Inst. med. Res.* **6** : 323 (*Simulium*).  
Holotype ♀, SOUTH AFRICA (TRANSVAAL) : SAIMR, Johannesburg.
- marlieri** Grenier, 1950, *Bull. Soc. Path. exot.* **43** : 97 (*Simulium*).  
Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : IP, Paris.
- masabae** Gibbins, 1934, *Trans. R. ent. Soc. Lond.* **82** : 79 (*Simulium*).  
Holotype ♀, UGANDA : BMNH, London.
- mcmahoni** de Meillon, 1940, *E. Afr. med. J.* **16** : 446 (*Simulium*).  
Holotype ♂, KENYA : SAIMR, Johannesburg.
- medusaeformis** Pomeroy, 1920, *Ann. Mag. nat. Hist.* (9) **6** : 76 (*Simulium*).  
Holotype ♂, CAMEROUN REPUBLIC : BMNH, London.
- merops** de Meillon, 1950, *Proc. R. ent. Soc. Lond.* (B) **19** : 14 (*Simulium*).  
Holotype ♂, SOUTH AFRICA (CAPE PROVINCE) : SAIMR, Johannesburg.
- milloti** Grenier & Doucet, 1949, *Mém. Inst. scient. Madagascar* (A) **3** : 307 (*Simulium*).  
Syntypes ♀, pupae, MALAGASY REPUBLIC (MADAGASCAR) : IP, Paris.

**monoceros** Roubaud & Grenier, 1943, *Bull. Soc. Path. exot.* **36** : 289 (*Simulium*).

Syntypes ♂, ♀ pupae, GUINEA : IP, Paris.

**morotoensis** McCrae & Prentice, 1965, *Proc. R. ent. Soc. Lond.* (B) **34** : 53 (*Paracnephia*). Holotype ♂, UGANDA : BMNH, London.

**muspratti** Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 30 (*Cnephia*). Holotype ♂, SOUTH AFRICA (CAPE PROVINCE) : SAIMR, Johannesburg.

**narcaeus** de Meillon, 1950, *Proc. R. ent. Soc. Lond.* (B) **19** : 16 (*Simulium*). Holotype ♂, SOUTH AFRICA (NATAL) : SAIMR, Johannesburg.

**natalensis** de Meillon, 1950, *Proc. R. ent. Soc. Lond.* (B) **19** : 14 (*Simulium*). Holotype ♂, SOUTH AFRICA (NATAL) : SAIMR, Johannesburg.

**neavei** Roubaud, 1915, *Bull. Soc. ent. Fr.* **1915** : 293 (*Simulium*). LECTOTYPE ♀ [by present designation], UGANDA : BMNH, London.

Roubaud described *neavei* from thirteen female specimens collected by Neave and stated to be in the British Museum collection. Six of these female syntypes now exist in the collection of BMNH, London, and one with data 'Uganda Prot. Western Ankole. 4500-5000 ft. 10-14, Oct. 1911. S. A. Neave' has been labelled and is here designated as lectotype.

**neireti** Roubaud, 1905, *Bull. Mus. natn. Hist. nat., Paris* **11** : 425 (*Simulium*). Syntypes ♀, MALAGASY REPUBLIC (MADAGASCAR) : MNHN, Paris.

**ngabogei** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 108 (*Simulium*). Syntypes ♂, ♀ pupae, RWANDA : MRAC, Tervuren.

**nigritarsis** Coquillett, 1902, *Proc. U.S. natn. Mus.* **24** : 27 (*Simulium*). Holotype ♀, SOUTH AFRICA (CAPE PROVINCE) : USNM, Washington.

**nili** Gibbins, 1934, *Trans. R. ent. Soc. Lond.* **82** : 74 (*Simulium*). Holotype ♀, UGANDA : BMNH, London.

**nyasalandicum** de Meillon, 1930, *Bull. ent. Res.* **21** : 190 (*Simulium*). LECTOTYPE ♀ [by present designation], MALAWI : BMNH, London.

De Meillon (*loc. cit.*) described *nyasalandicum* from five female syntypes, all of which are in BMNH, London ; one specimen has been labelled and is here designated as lectotype. Data of the lectotype and paralectotypes are : 'Nyasaland Protectorate : Mt. Mlanje. 20.i.1914. S. A. Neave'. The lectotype bears, in addition, a circular red-bordered 'Type' label with the inscription 'Simulium nyasalandicum Roubaud' in Austen's writing : as de Meillon noted in the original description, the name was not published by Roubaud.

**obscurum** Gibbins, 1937, *Bull. ent. Res.* **28** : 289 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.

Name preoccupied in *Simulium* by *obscurum* Enderlein, 1924, see replacement name *Simulium cavum* Gibbins, 1938 : holotype of *obscurum* Gibbins labelled as *cavum*.

**occidentale** Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 56 (*Simulium*, as form of *alcocki* Pomeroy, 1922). Replacement name for *Simulium alcocki* var. *violaceum* Pomeroy, 1922, preoccupied by *Simulium violaceum* Enderlein, 1922. Lectotype ♂, NIGERIA : BMNH, London. (For designation see under *violaceum* Pomeroy).

- Name preoccupied in *Simulium* by *occidentale* Townsend, 1891, see *garnsi* **nom. n.**
- octospicae** Gibbins, 1937, *Bull. ent. Res.* **28** : 295 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- ovazzae** Grenier & Mouchet, 1959, *Bull. Soc. Path. exot.* **52** : 373 (*Simulium*). Holotype ♂, CAMEROUN REPUBLIC : IP, Paris.
- palmeri** Pomeroy, 1922, *Bull. ent. Res.* **12** : 462 (*Simulium*). Holotype ♂, NIGERIA : BMNH, London.
- pauliani** Grenier & Doucet, 1949, *Bull. Soc. Path. exot.* **42** : 587 (*Simulium*). Syntypes ♂, ♀, pupae, larvae, MALAGASY REPUBLIC (MADAGASCAR) : IP, Paris.
- phoroniformis** de Meillon, 1937, *Publs S. Afr. Inst. med. Res.* **7** : 399 (*Simulium*). Holotype ♂, SOUTH AFRICA (ZULULAND) : SAIMR, Johannesburg.
- pseudomedusaeformis** de Meillon, 1936, *Publs S. Afr. Inst. med. Res.* **7** : 212 (*Simulium*). Holotype ♂, SOUTH AFRICA (ZULULAND) : SAIMR, Johannesburg.
- renauxi** Wanson & Lebied, 1950, *Revue Zool. Bot. afr.* **43** : 309 (*Simulium*). Syntypes ♀, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.
- rhodesianum** Crosskey, 1968, *J. nat. Hist.* **2** : 488 (*Prosimulium*). Holotype ♂, RHODESIA : BMNH, London.
- rhodesiensis** de Meillon, 1942, *J. ent. Soc. sth. Afr.* **5** : 90 (*Simulium*). Holotype ♂, RHODESIA : SAIMR, Johannesburg.
- rickenbachi** Germain, Grenier & Mouchet, 1966, *Bull. Soc. Path. exot.* **59** : 133 (*Simulium*). Holotype ♂, CAMEROUN REPUBLIC : IP, Paris.
- rodhaini** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 101 (*Simulium*). Syntypes ♂, ♀, pupae, RWANDA : MRAC, Tervuren and BMNH, London.
- rotundum** Gibbins, 1936, *Trans. R. ent. Soc. Lond.* **85** : 241 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- roubaudi** Grenier & Rageau, 1949, *Bull. Soc. Path. exot.* **42** : 514 (*Simulium*). Syntypes ♂, pupae, larvae, CAMEROUN REPUBLIC : IP, Paris.
- ruandae** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 115 (*Simulium*). Syntypes ♂, ♀, pupae, RWANDA : MRAC, Tervuren and BMNH, London.
- ruficorne** Macquart, 1838, *Mém. Soc. Sci. Agric. Lille* **1838** : 88. *Diptères exot.* **1** : 84 (*Simulium*). Holotype ♂, ÎLE BOURBON [=La RÉUNION] : lost.
- rutherfordi** de Meillon, 1937, *Publs S. Afr. Inst. med. Res.* **7** : 397 (*Simulium*). Holotype ♂, SOUTH AFRICA (ZULULAND) : SAIMR, Johannesburg.
- ruwenzoriensis** Gibbins, 1934, *Trans. R. ent. Soc. Lond.* **82** : 63 (*Simulium*). Holotype ♀, UGANDA : lost (♂, ♀ paratypes with same data as holotype in BMNH, London).
- scapulata** Enderlein, 1935, *Sber. Ges. naturf. Freunde Berl.* **1935** : 359 (*Psilocnetha*). Holotype ♀, EGYPT : ZMHU, Berlin.
- schoutedeni** Wanson, 1947, *Revue Zool. Bot. afr.* **40** : 203 (*Simulium*). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren and BMNH, London (1 ♀).
- schwetzi** Wanson, 1947, *Revue Zool. Bot. afr.* **40** : 200 (*Simulium*). Holotype pupa, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.

- sexiens** de Meillon, 1944, *Proc. R. ent. Soc. Lond.* (B) **13** : 119 (*Simulium*, as variety of *hirsutum* Pomeroy, 1922). Holotype ♂ pupal pelt, KENYA : SAIMR, Johannesburg.
- sextumdecimum** Luna de Carvalho, 1962, *Publçoes cult. Co. Diam. Angola*, No. 60 : 19 (*Simulium*, as form of *alcocki* Pomeroy, 1922). [Unavailable name under Article 15 of *International Code of Zoological Nomenclature*, 1961].
- shoae** Grenier & Ovazza, 1956, *Bull. Soc. Path. exot.* **49** : 190 (*Simulium*, as form of *dentulosum* Roubaud, 1915). Syntypes pupae and larvae, ETHIOPIA : IP, Paris.
- simplex** Gibbins, 1936, *Trans. R. ent. Soc. Lond.* **85** : 232 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- speculiventre** Enderlein, 1914, *Trans. Linn. Soc. Lond. (Zool.)*, Ser. 2, **16** : 374 (*Simulium*). Lectotype ♂, SEYCHELLES : BMNH, London, Lectotype designation by Crosskey, 1966, *Ann. Mag. nat. Hist.* (13) **8** (1965) : 130.
- squamosum** Enderlein, 1921, *Sber. Ges. naturf. Freunde Berl.* **1921** : 80 (*Edwardsellum*). Holotype ♀, CAMEROUN REPUBLIC : ZMHU, Berlin.
- starmuhlneri** Grenier & Grjébine, 1963, *Bull. Soc. Path. exot.* **56** : 1055 (*Simulium*). Holotype ♂, MALAGASY REPUBLIC (MADAGASCAR) : IP, Paris.
- tangae** Smart, 1944, *Proc. R. ent. Soc. Lond.* (B) **13** : 132 (*Simulium*). Replacement name for *Simulium limbatum* Enderlein, 1921, preoccupied by *Simulium limbatum* Knab, 1915. Lectotype ♂, TANZANIA (TANGANYIKA) : ZMHU, Berlin.
- taylori** Gibbins, 1938, *Ann. trop. Med. Parasit.* **32** : 24 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- tentaculum** Gibbins, 1936, *Trans. R. ent. Soc. Lond.* **85** : 228 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- thornei** de Meillon, 1955, *S. Afr. anim. Life* **2** : 350 (*Cnephia*). Holotype ♂, SOUTH AFRICA (CAPE PROVINCE) : SAIMR, Johannesburg.
- tisiphone** de Meillon, 1936, *Publs S. Afr. Inst. med. Res.* **7** : 210 (*Simulium*). Holotype ♂, SOUTH AFRICA (ZULULAND) : SAIMR, Johannesburg.
- touffeum** Gibbins, 1937, *Bull. ent. Res.* **28** : 292 (*Simulium*). Holotype ♂, UGANDA : BMNH, London.
- tridens** Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 138 (*Simulium*, as form of *griseicolle* Becker, 1903). Holotype ♂, GHANA : BMNH, London.
- trisphaerae** Wanson & Henrard, 1944, *E. Afr. med. J.* **21** : 43 (*Simulium*, as variety of *griseicolle* Becker, 1903). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.
- turneri** Gibbins, 1938, *Ann. trop. Med. Parasit.* **32** : 22 (*Simulium*). Holotype ♀, SOUTH AFRICA (CAPE PROVINCE) : BMNH, London.
- ugandae** Gibbins, 1934, *Trans. R. ent. Soc. Lond.* **82** : 88 (*Simulium*). Holotype ♀, UGANDA : possibly lost (♂♂ and ♀♀ in BMNH, London with identical data and presumed original material : none labelled by Gibbins as holotype, and most bearing determination labels as *medusaeformis* in Gibbins' writing, these labels probably added after the description of *ugandae*).
- unicornutum** Pomeroy, 1920, *Ann. Mag. nat. Hist.* (9) **6** : 79 (*Simulium*). Holotype pupa [slide-mounted], CAMEROUN REPUBLIC : BMNH, London.

- urundiensis** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 122 (*Simulium*, as variety of *adersi* Pomeroy, 1922). Syntypes ♂, pupae, BURUNDI : MRAC, Tervuren and BMNH, London (1 ♂).
- vangilsi** Wanson, 1947, *Revue Zool. Bot. afr.* **40** : 207 (*Simulium*). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren and BMNH, London (1 ♂).
- vargasi** Grenier & Rageau, 1949, *Bull. Soc. Path. exot.* **42** : 518 (*Simulium*). Syntypes ♂, pupae, larvae, CAMEROUN REPUBLIC : IP, Paris.
- vilhenai** Luna de Carvalho, 1962, *Publçoes cult. Co. Diam. Angola*, No. 60 : 44 (*Simulium*). Syntypes ♂, ♀, pupae, larvae, ANGOLA : MD, Dundo and BMNH, London.
- violaceum** Pomeroy, 1922, *Bull. ent. Res.* **12** : 460 (*Simulium*, as variety of *alcocki* Pomeroy, 1922). LECTOTYPE pupa [by present designation] (ring-mounted on pin), NIGERIA : BMNH, London.

Pomeroy described *violaceum* from an unstated number of pupae and reared adults, distinguishing the variety from *alcocki* type-form by the 10-filamented pupal gill ; the types, unspecified, were stated to be in British Museum. The existing type-material in BMNH, London consists of one reared ♂, one reared ♀, legs of a reared ♀, and a cocoon and pupal parts (including gills), all material representing syntypes in poor condition on four mounts in the pinned collection. The pupal specimen (showing the distinguishing gill-character) has been labelled and is here designated as lectotype : the data are as follows :— a type-written label reading 'Ibadan Nigeria' with the hand-written date '6.xii.20', and the label 'S. alcocki var. violaceum Pom. Pupal filaments' in Pomeroy's writing.

Name preoccupied by *Simulium violaceum* Enderlein, 1922, see replacement name *occidentale* Freeman & de Meillon, 1953.

- voltae** Grenier, Ovazza & Valade, 1960, *Bull. Inst. fr. Afr. noire* **22** : 905 (*Simulium*, as form of *dentulosum* Roubaud, 1915). Syntype pupae, UPPER VOLTA : IP, Paris.
- vorax** Pomeroy, 1922, *Bull. ent. Res.* **12** : 461 (*Simulium*). Neotype ♀, TANZANIA (TANGANYIKA) : BMNH, London. Neotype designation by Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 184.
- vulcani** Fain, 1950, *Revue Zool. Bot. afr.* **43** : 118 (*Simulium*). Syntypes ♂, ♀, pupae, RWANDA : MRAC, Tervuren and BMNH, London (1 ♂, 1 pupa).
- wellmanni** Roubaud, 1906, *Bull. Mus. natn. Hist. nat., Paris* **12** : 519 (*Simulium*). LECTOTYPE ♀ [by present designation], ANGOLA : BMNH, London.

The original description of *wellmanni* was based on four female syntypes ('Quatre exemplaires femelles provenant de l'Angola et recueillis par le docteur Wellmann en avril 1905'), stated to be from the British Museum collection. Only one syntype now exists in BMNH, London (referred to in error as holotype by Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 207), and this has been labelled and is here designated as lectotype. Lectotype data are : a hand-written label reading "'Bulu-Bulu" Plain, Bihe, Angola. W. Africa. April, 1905. Dr. F. C. Wellman.' ; a Roubaud determination label as *wellmanni* ; a printed

' ♀ ' sex label ; a circular red-bordered ' Type ' label with the inscription ' *Simulium wellmanni* Roubaud ' in Austen's writing and a hand-written label reading ' Native name " Ohomono ". These tiny flies bite viciously and are dreaded by naked porters. Their bite leaves a large raised wheal, with a small red spot in the centre. It itches for several days. (Note by donor) '.

**weyeri** Garms & Häusermann, 1968, *Revue Zool. Bot. afr.* **78** : 67 (*Simulium*).

Holotype ♂ ex pupa, TANZANIA : ZSM, Hamburg.

**wolfsi** Wanson & Henrard, 1944, *E. Afr. med. J.* **21** : 38 (*Simulium*). Syntypes ♂, ♀, pupae, DEMOCRATIC REPUBLIC OF CONGO : MRAC, Tervuren.

**woodi** de Meillon, 1930, *Bull. ent. Res.* **21** : 190 (*Simulium*). LECTOTYPE ♀ [by present designation], MALAWI : BMNH, London.

The original description of *woodi* was based on four female syntypes collected by Wood in September, 1917, at Cholo, Nyasaland. Two of the syntypes (one pinned, the other slide-mounted in parts) are in BMNH, London, and the pinned specimen (labelled ' -ix.17 Cholo Nyasaland. 3000 ' . R. C. Wood. On wooded hill 980 ' on circular white label) has been labelled and is here designated as lectotype. Two other females are in BMNH collection from the type-locality, also collected by Wood, but these specimens bear the date 26.xi.20 : as the data is different from that cited by de Meillon in the original description they are not considered to be part of the syntypic series.

**zombaensis** Freeman & de Meillon, 1953, *Sim. Ethiop. Reg.* : 194 (*Simulium*, as form of *taylori* Gibbins, 1938). Holotype ♂ pupa, MALAWI : BMNH, London.

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## LIST OF SPECIES ON WHICH THE TEXT-FIGURES ARE BASED

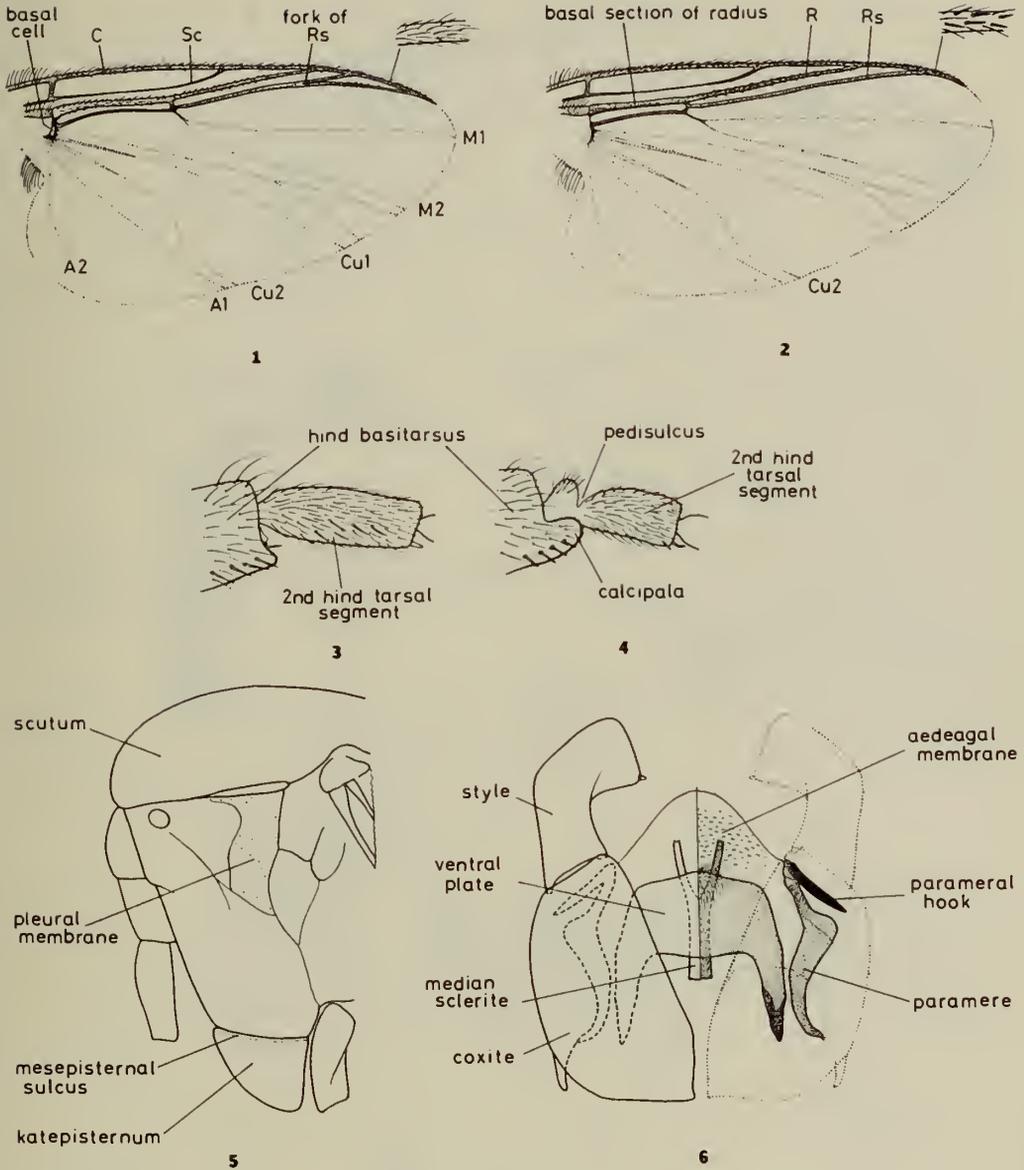
A few of the accompanying text-figures numbered from 1-331 are generalized drawings designed to show morphological features used in taxonomy, but most are based on particular species within the supraspecific taxa illustrated. The following list shows the species used for the illustrations against the appropriate text-figure numbers.

22	<i>rhodesianum</i>	28	<i>thornei</i>
23	<i>muspratti</i>	29	<i>thornei</i>
24	<i>thornei</i>	30	<i>brincki</i>
25	<i>turneri</i>	31	<i>rhodesianum</i>
26	<i>morotoense</i>	32	<i>thornei</i>
27	<i>morotoense</i>	33	<i>muspratti</i>

34	<i>harrisoni</i>	89	<i>neavei</i>
35	<i>blanci</i>	90	<i>dentulosum</i>
38	<i>rhodesianum</i>	91	<i>debegene</i>
39	<i>damarense</i>	92	<i>medusaeforme</i>
40	<i>barnardi</i>	93	<i>mediterraneum</i>
41	<i>brincki</i>	94	<i>ornatum</i>
42	<i>rhodesianum</i>	95	<i>griseicolle</i>
43	<i>muspratti</i>	96	<i>hissetteum</i>
44	<i>brincki</i>	97	<i>tentaculum</i>
45	<i>rhodesianum</i>	98	<i>ituriense</i>
47	<i>rhodesianum</i>	99	<i>cervicornutum</i>
48	<i>rhodesianum</i>	100	<i>costatum</i>
49	<i>damarense</i>	101	<i>ruficorne</i>
50	<i>morotoense</i>	103	<i>loutetense</i>
51	<i>thornei</i>	104	<i>imerinae</i>
52	<i>brincki</i>	105	<i>neavei</i>
53	<i>muspratti</i>	106	<i>berneri</i>
54	<i>rhodesianum</i>	107	<i>griseicolle</i>
55	<i>muspratti</i>	108	<i>nili</i>
56	<i>muspratti</i>	109	<i>dentulosum</i>
58	<i>gariepense</i>	110	<i>berghei</i>
60	<i>gariepense</i>	111	<i>debegene</i>
62	<i>gariepense</i>	112	<i>hirsutilateris</i>
64	<i>gariepense</i>	113	<i>mediterraneum</i>
67	<i>gariepense</i>	114	<i>colasbelcouri</i>
68	<i>gariepense</i>	115	<i>wellmanni</i>
71	<i>atlanticum</i>	116	<i>hargreavesi</i>
72	<i>mediterraneum</i>	117	<i>albivirgulatum</i>
73	<i>bezzii</i>	118	<i>vilhenai</i>
74	<i>nitidifrons</i>	119	<i>ornatum</i>
75	<i>nitidifrons</i>	120	<i>hissetteum</i>
76	<i>chutteri</i>	121	<i>merops</i>
77	<i>damnosum</i>	122	<i>kenyae</i>
78	<i>bequaerti</i>	123	<i>rutherfoordi</i>
79	<i>ruficorne</i>	125	<i>ruficorne</i>
80	<i>neavei</i>	126	<i>hirsutum</i>
81	<i>copleyi</i>	127	<i>neavei</i>
82	<i>damnosum</i>	128	<i>berneri</i>
83	<i>vorax</i>	129	<i>iphias</i>
84	<i>mediterraneum</i>	130	<i>griseicolle</i>
85	<i>bezzii</i>	131	<i>berghei</i>
86	<i>intermedium</i>	132	<i>dentulosum</i>
87	<i>griseicolle</i>	133	<i>vorax</i>
88	<i>nigritarse</i>	134	<i>bovis</i>

135	<i>albivirgulatum</i>	190	<i>palmeri</i>
136	<i>machadoi</i>	191	<i>leberrei</i>
137	<i>damnosum</i>	192	<i>unicornutum</i>
138	<i>bezzii</i>	193	<i>hirsutum</i>
139	<i>nitidifrons</i>	194	<i>adersi</i>
140	<i>allaeri</i>	195	<i>neavei</i>
141	<i>bequaerti</i>	196	<i>tentaculum</i>
143	<i>nigritarse</i>	197	<i>copleyi</i>
144	<i>loveridgei</i>	198	<i>lumbwanum</i>
145	<i>neavei</i>	199	<i>berneri</i>
146	<i>copleyi</i>	200	<i>iphias</i>
147	<i>debegene</i>	201	<i>ambositrac</i>
148	<i>imerinae</i>	202	<i>imerinae</i>
149	<i>dentulosum</i>	203	<i>dentulosum</i>
150	<i>damnosum</i>	204	<i>octospicae</i>
151	<i>mediterraneum</i>	205	<i>berghei</i>
152	<i>bovis</i>	206	<i>hessei</i>
153	<i>wellmanni</i>	207	<i>mediterraneum</i>
154	<i>bifila</i>	208	<i>gyas</i>
155	<i>nitidifrons</i>	209	<i>machadoi</i>
160	<i>wellmanni</i>	210	<i>damnosum</i>
161	<i>iphias</i>	211	<i>hargreavesi</i>
162	<i>vorax</i>	212	<i>vorax</i>
163	<i>debegene</i>	213	<i>futaense</i>
169	<i>copleyi</i>	214	<i>albivirgulatum</i>
170	<i>lumbwanum</i>	215	<i>bovis</i>
172	<i>copleyi</i>	216	<i>wellmanni</i>
173	<i>lumbwanum</i>	217	<i>bezzii</i>
174	<i>ruficorne</i>	218	<i>bezzii</i>
175	<i>loveridgei</i>	219	<i>gaudi</i>
176	<i>loutetense</i>	220	<i>nitidifrons</i>
177	<i>narcaeum</i>	221	<i>bifila</i>
178	<i>rutherfordi</i>	222	<i>griseicolle</i>
179	<i>speculiventre</i>	223	<i>gariépense</i>
180	<i>starmuhlneri</i>	224	<i>unicornutum</i>
181	<i>bequaerti</i>	226	<i>vorax</i>
182	<i>hisseteum</i>	228	<i>bovis</i>
183	<i>alcocki</i>	230	<i>damnosum</i>
184	<i>kenyae</i>	232	<i>unicornutum</i>
185	<i>mcmahoni</i>	233	<i>adersi</i>
186	<i>schwetzi</i>	234	<i>kenyae</i>
187	<i>cervicornutum</i>	235	<i>ruficorne</i>
188	<i>vangilsi</i>	236	<i>loutetense</i>
189	<i>blacklocki</i>	237	<i>dentulosum</i>

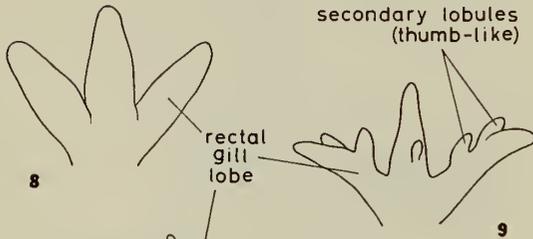
238	<i>hargreavesi</i>	272	<i>ruficorne</i>
239	<i>colasbelcouri</i>	273	<i>alcocki</i>
240	<i>damnosum</i>	274	<i>griseicollae</i>
241	<i>costatum</i>	275	<i>dentulosum</i>
242	<i>loveridgei</i>	276	<i>berghei</i>
243	<i>ruficorne</i>	277	<i>ambositrae</i>
244	<i>duboisi</i>	278	<i>hargreavesi</i>
245	<i>loutetense</i>	279	<i>vorax</i>
246	<i>alcocki</i>	280	<i>bovis</i>
247	<i>harrisoni</i>	281	<i>albivirgulatum</i>
248	<i>unicornutum</i>	282	<i>damnosum</i>
249	<i>kenyae</i>	283	<i>neavei</i>
250	<i>adersi</i>	284	<i>neavei</i>
251	<i>neavei</i>	285	<i>copleyi</i>
252	<i>berneri</i>	286	<i>copleyi</i>
253	<i>dentulosum</i>	287	<i>albivirgulatum</i>
254	<i>berghei</i>	290	<i>ambositrae</i>
255	<i>imerinae</i>	291	<i>cervicornutum</i>
256	<i>mediterraneum</i>	292	<i>neavei</i>
257	<i>vorax</i>	293	<i>lumbwanum</i>
258	<i>hargreavesi</i>	294	<i>vorax</i>
259	<i>albivirgulatum</i>	295	<i>berghei</i>
260	<i>chutteri</i>	296	<i>imerinae</i>
261	<i>damnosum</i>	297	<i>neavei</i>
262	<i>tridens</i>	298	<i>lumbwanum</i>
263	<i>bezzii</i>	299	<i>copleyi</i>
264	? <i>intermedium</i>	300	<i>vorax</i>
265	<i>lumbwanum</i>	301	<i>berghei</i>
266	<i>copleyi</i>	302	<i>ambositrae</i>
267	<i>berneri</i>	305	<i>gariépense</i>
268	<i>neavei</i>	306	<i>gariépense</i>
269	<i>loutetense</i>	307	<i>gariépense</i>
270	<i>speculiventre</i>	308	<i>gariépense</i>
271	<i>loveridgei</i>		



FIGS. 1-6. Structures of adult Simuliidae and their terms. Wing in forms (1) with basal cell and forked *Rs*, and (2) in forms without basal cell and simple *Rs*. Second hind tarsal segment and apex of hind basitarsus in forms (3) without pedisulcus or calcipala, and (4) in forms with pedisulcus and calcipala. 5, left lateral view of anterior part of thorax. 6, male hypopygium in ventral view (coxite and style shown only in outline on one side).



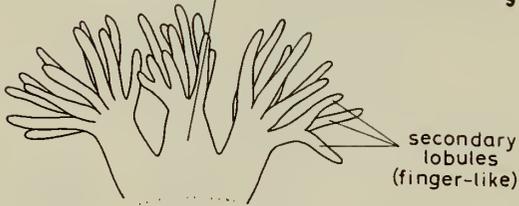
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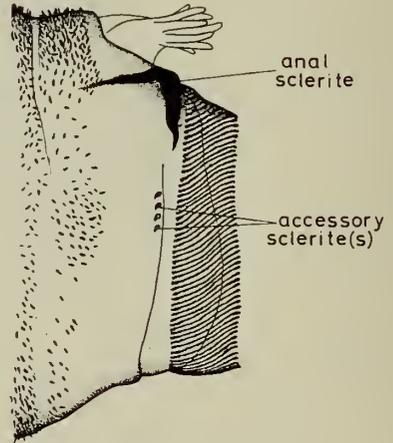
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secondary lobules  
(thumb-like)rectal gill  
lobe

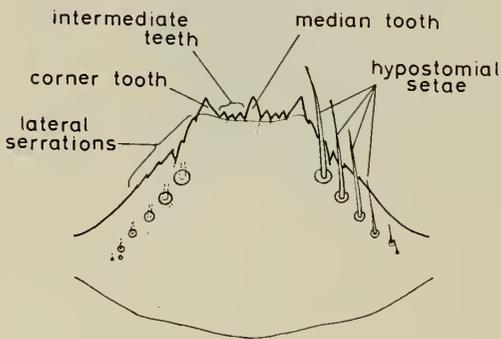
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10

secondary  
lobules  
(finger-like)

11

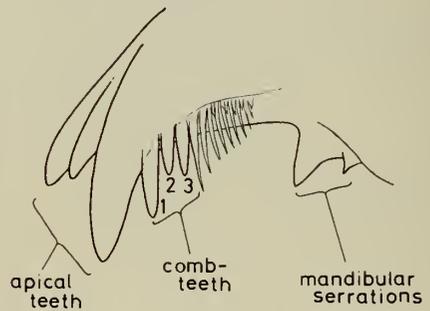
anal  
scleriteaccessory  
sclerite(s)

12

intermediate  
teeth

median tooth

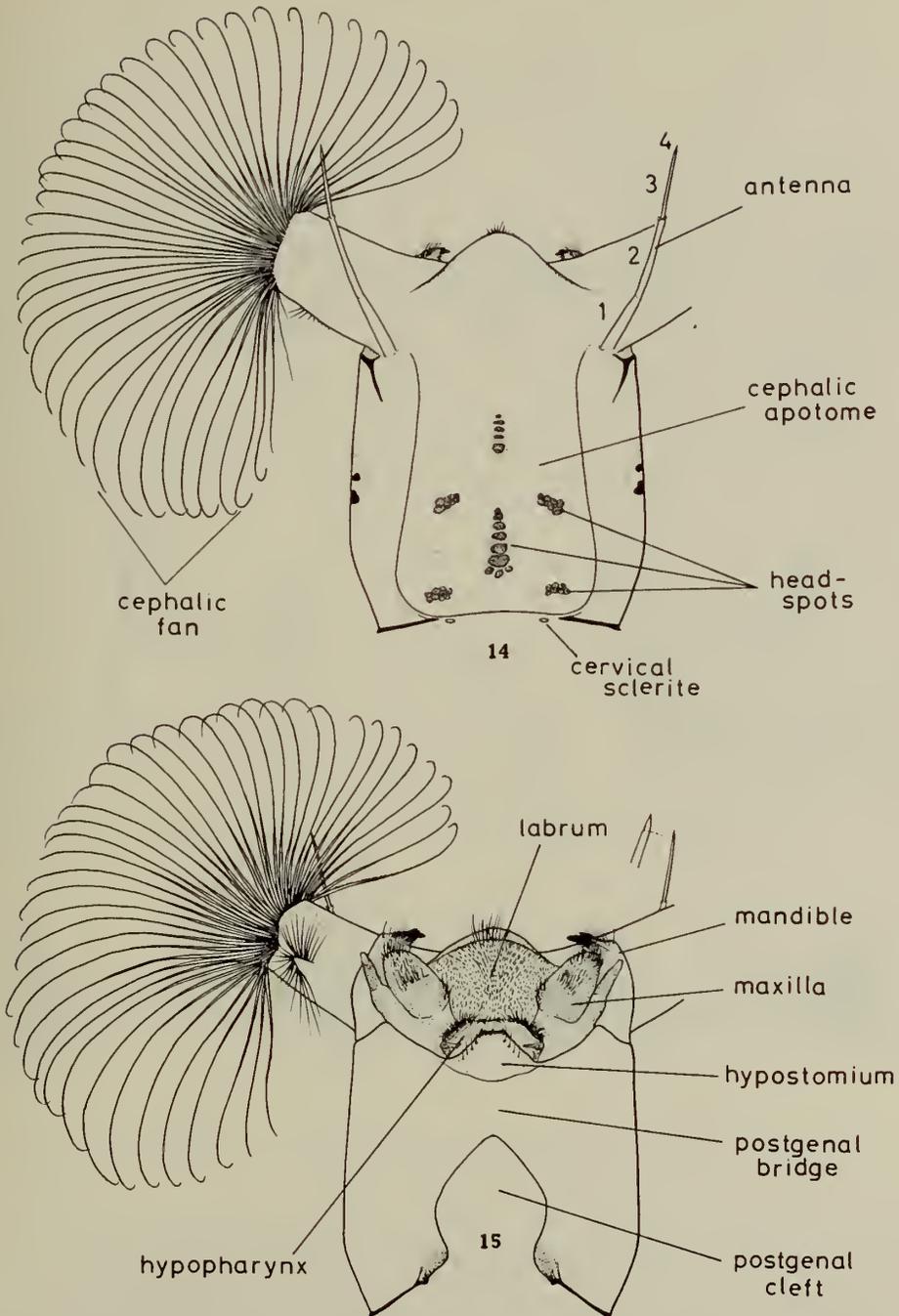
corner tooth

hypostomial  
setaelateral  
serrations

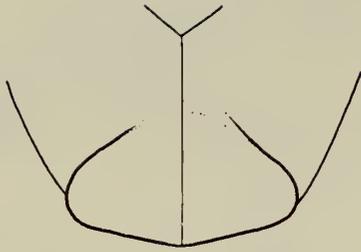
13

apical  
teethcomb-  
teethmandibular  
serrations

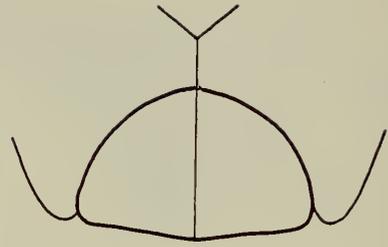
FIGS. 7-13. Structures of larval Simuliidae and their terms. 7, mature larva in profile. 8-10, forms of rectal gill. 11, lateral view of terminal abdominal structures. 12, hypostomium. 13, apex of the mandible.



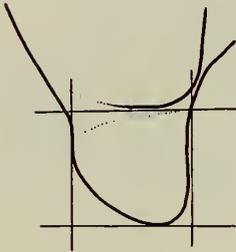
FIGS. 14 and 15. Dorsal view (14) and ventral view (15) of head structures of a Simuliid larva and their terms. The cephalic fan is shown for one side only.



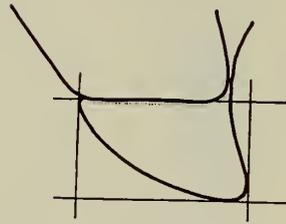
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17



18



19

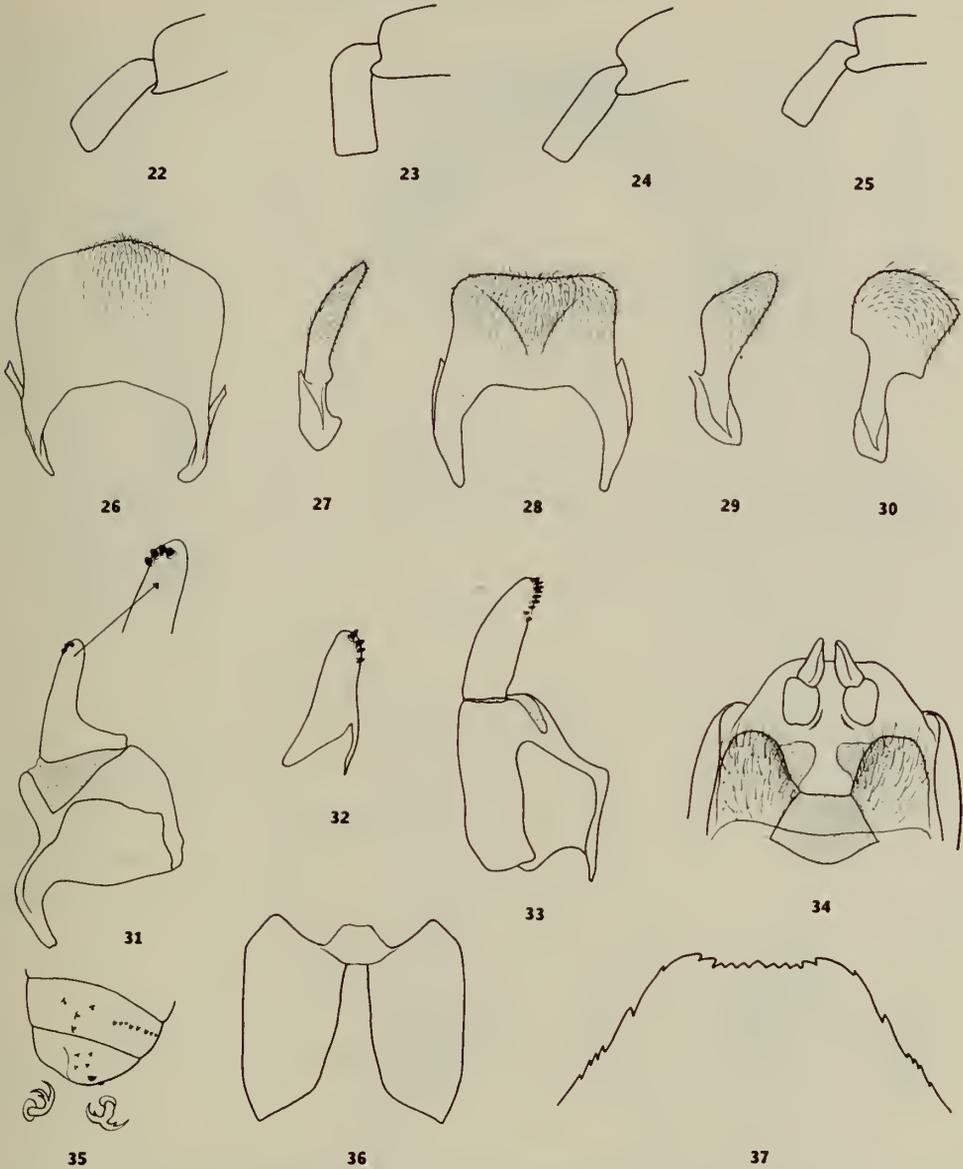


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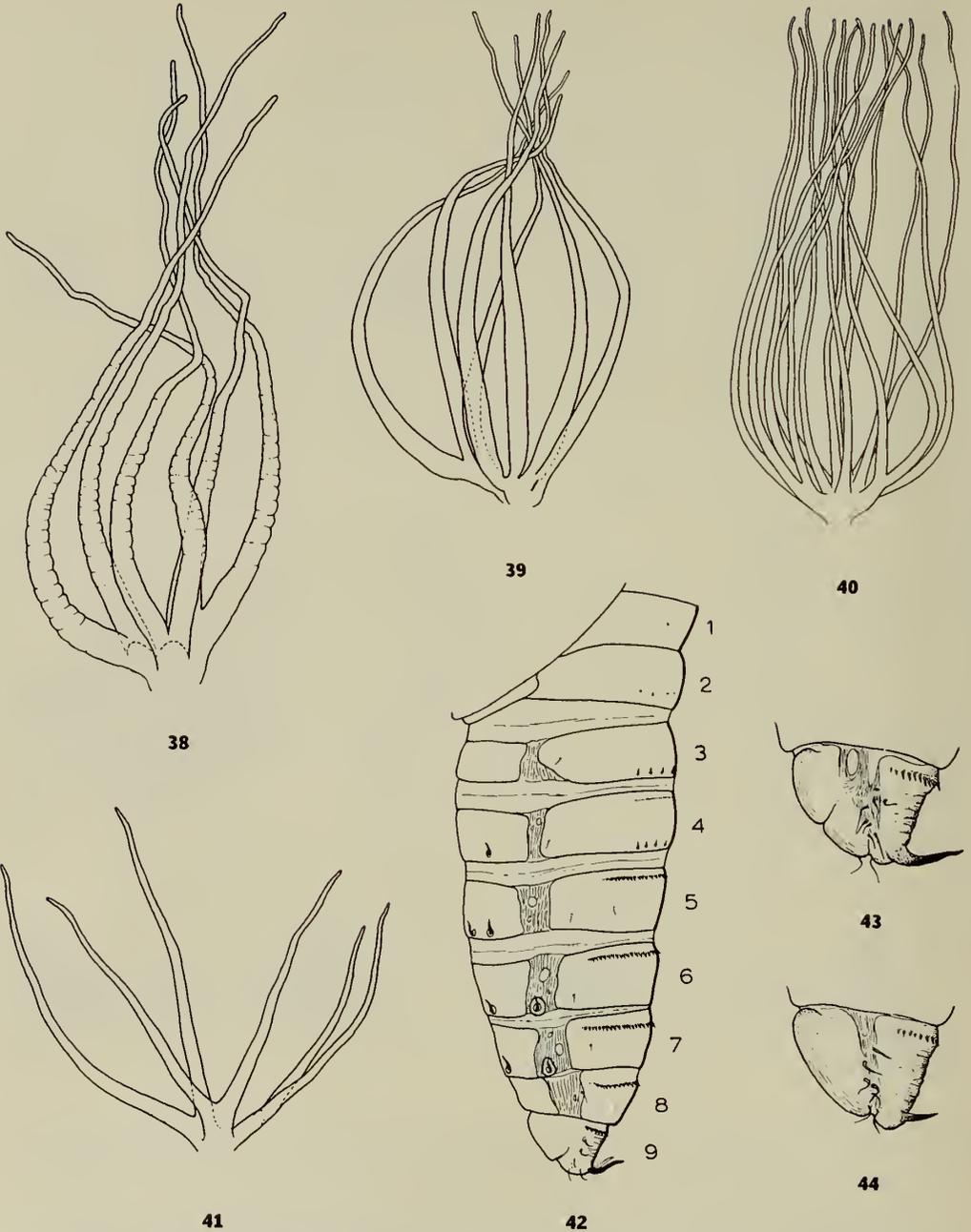


21

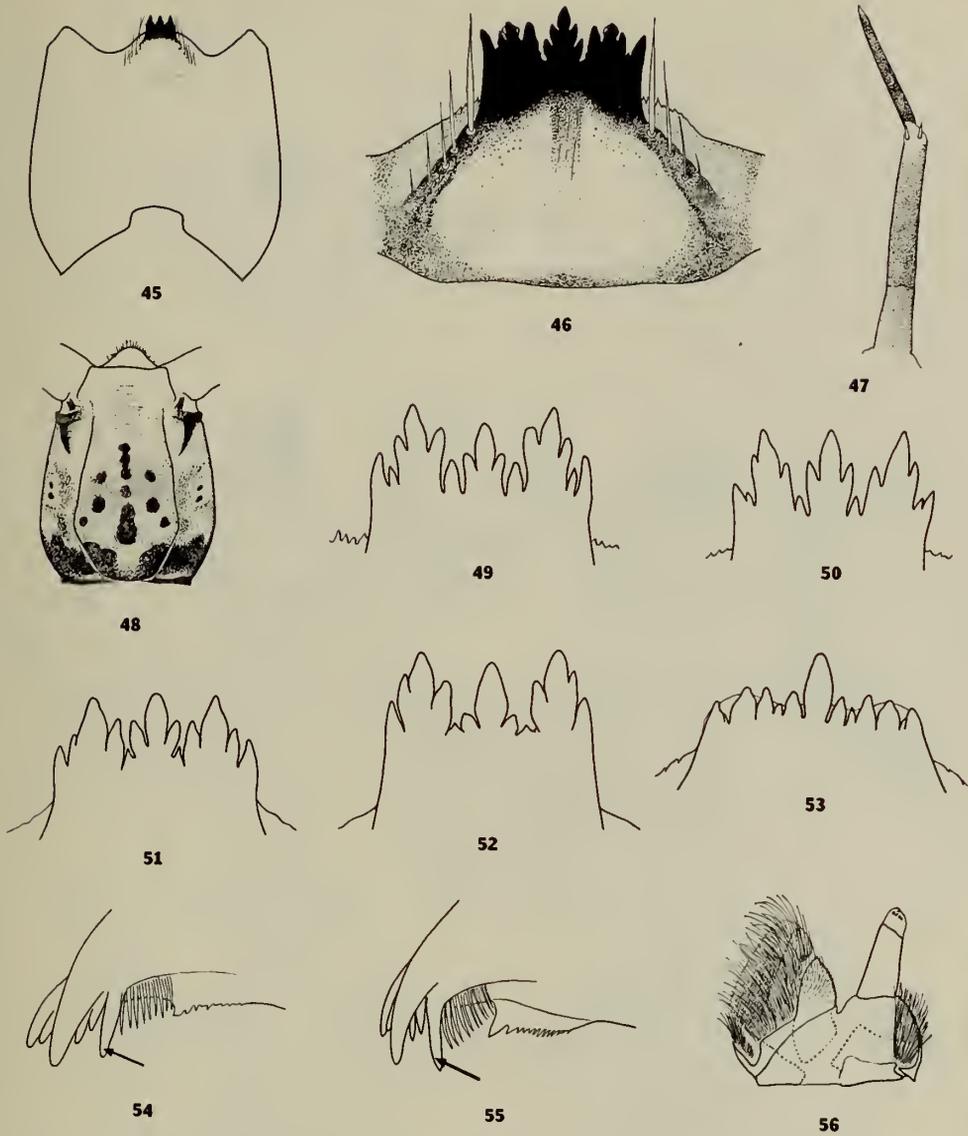
FIGS. 16-21. Showing differences between typical Prosimuliini and typical Simuliini. 16 and 17, ventral view of mesepisternal sulcus and katepisternum in (16) Prosimuliini and (17) Simuliini. 18 and 19, view in profile of katepisternum and mesepisternal sulcus in (18) Prosimuliini and (19) Simuliini. 20 and 21, posterior margin of head and cervical sclerites of mature larva in (20) many Prosimuliini and in (21) Simuliini. All figures slightly schematic.



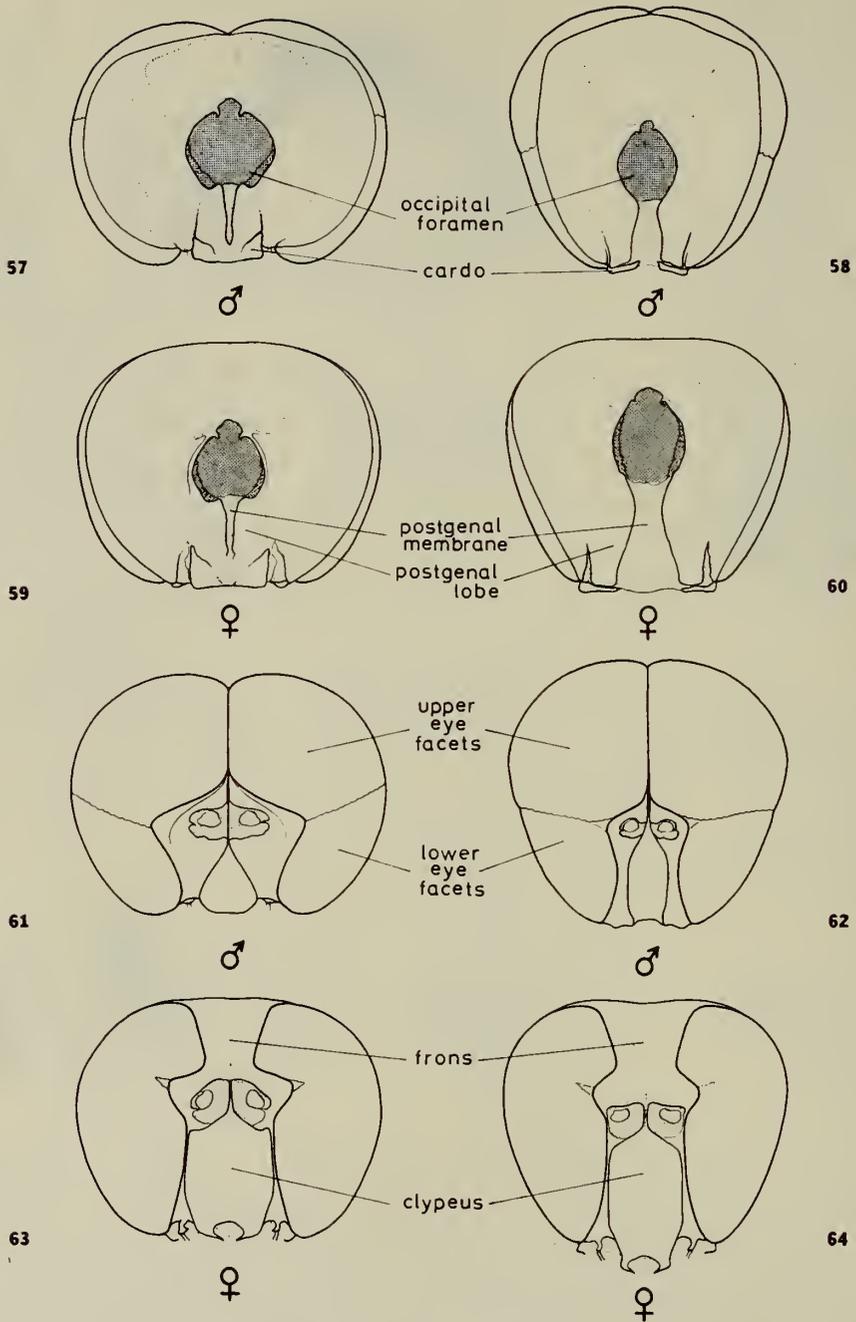
FIGS. 22-37. (22-34) Adult characters of African *Prosimulium* s.l. 22-25, degree of development of the calcipala in (22) *Procnephia*; (23 and 24) *muspratti*-group of *Paracnephia*; (25) *turneri*-group of *Paracnephia*. 26-30, male ventral plate of (26) typical *Procnephia* in ventral view; (27) typical *Procnephia* in profile; (28) *Paracnephia* in ventral view; (29 and 30) *Paracnephia* in profile. 31-33, coxite and style of (31) typical *Procnephia*, (32 and 33) *Paracnephia*. 34, female terminalia, ventral view, of *Procnephia* and *Paracnephia*. (35-37) Pupal and larval characters of *Metacnephia* gen. n.: (35) apex of pupal abdomen showing (with enlargement) biramous anchor-like hooklets (redrawn from Grenier & Theodorides (1953)); (36) form of larval postgenal cleft reaching forward to hypostomium; (37) typical form of apical teeth of hypostomium.



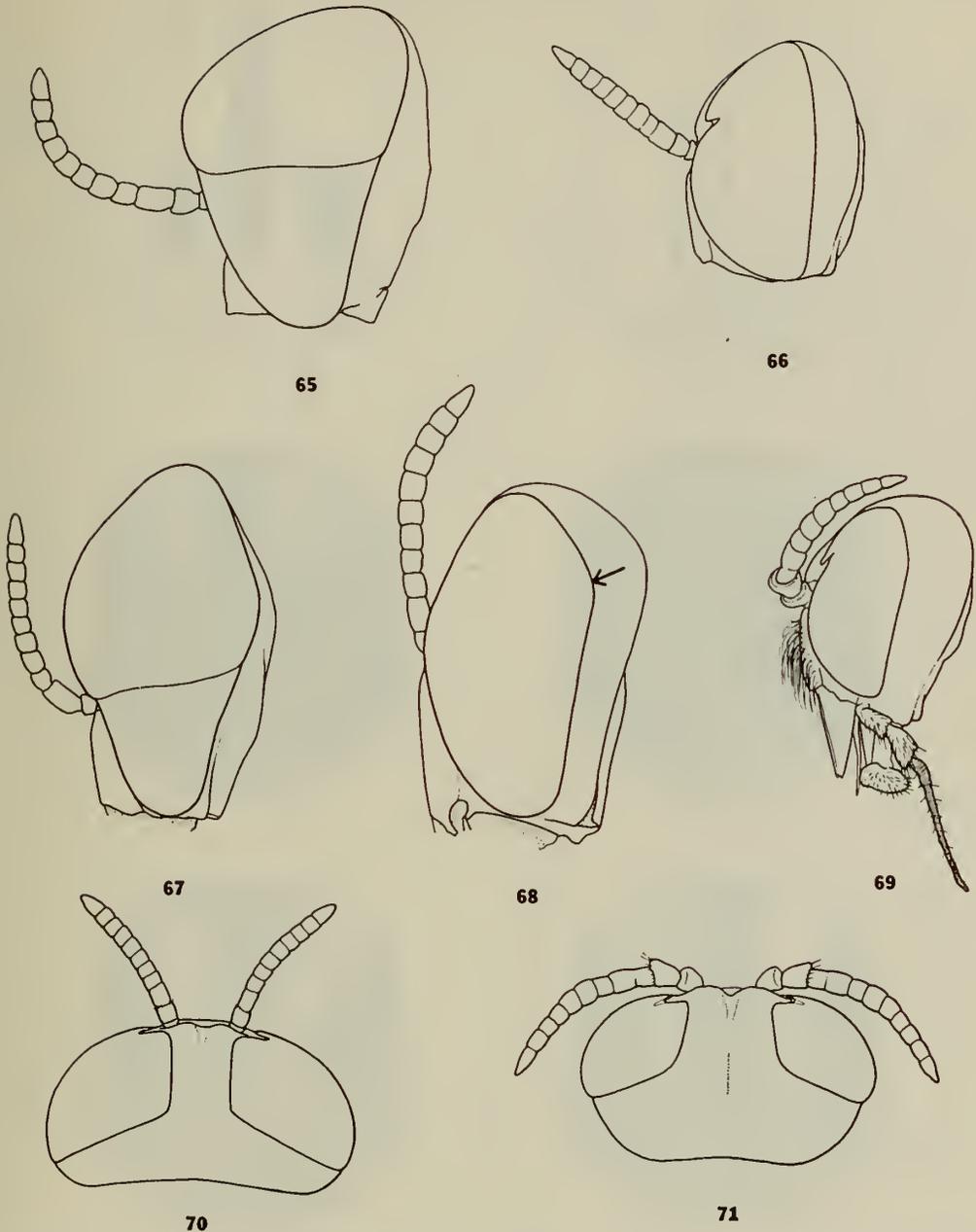
FIGS. 38-44. Pupal characters of African *Prosimulium* s.l. 38-41, form of pupal gill in (38 and 39) subgenus *Procnephia*; in (40) *muspratti*-group of subgenus *Paracnephia*, and (41) in *brincki*-group of *Paracnephia*. 42, lateral view of pupal abdomen in Ethiopian forms of *Prosimulium*. 43, form of pupal terminal hooks in most African *Prosimulium*. 44, form of pupal terminal hooks in *brincki*-group of subgenus *Paracnephia*.



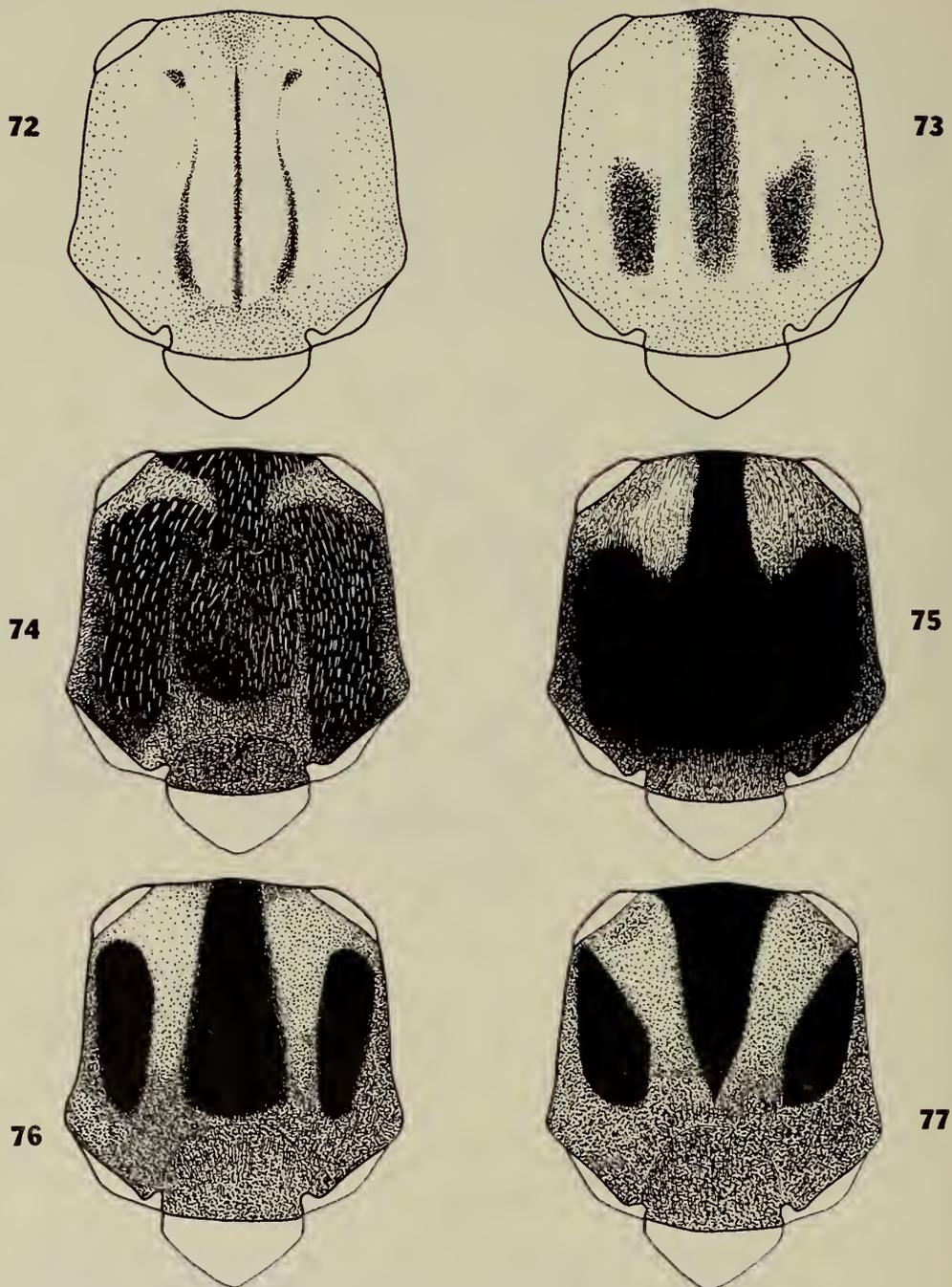
FIGS. 45-56. Larval characters of African *Prosimulium* s.l. 45, form of the postgenal cleft and elongate blackened apex of hypostomium. 46, typical form of the hypostomium. 47, antenna, showing short darkened third segment. 48, head of subgenus *Procnephia* showing head-spots and shape of cephalic apotome, cephalic fans omitted. 49-53, form of apical teeth of hypostomium in (49 and 50) subgenus *Procnephia* and in (51-53) subgenus *Paracnephia*. 54 and 55, apex of mandible showing usual form of mandibular serrations in (54) subgenus *Procnephia* and in (55) subgenus *Paracnephia*. 56, maxilla showing dense dark tuft of hairs near base of maxillary palp. The arrows in figures 54 and 55 draw attention to the enormously enlarged third comb-tooth of the mandible characteristic of *Prosimulium*.



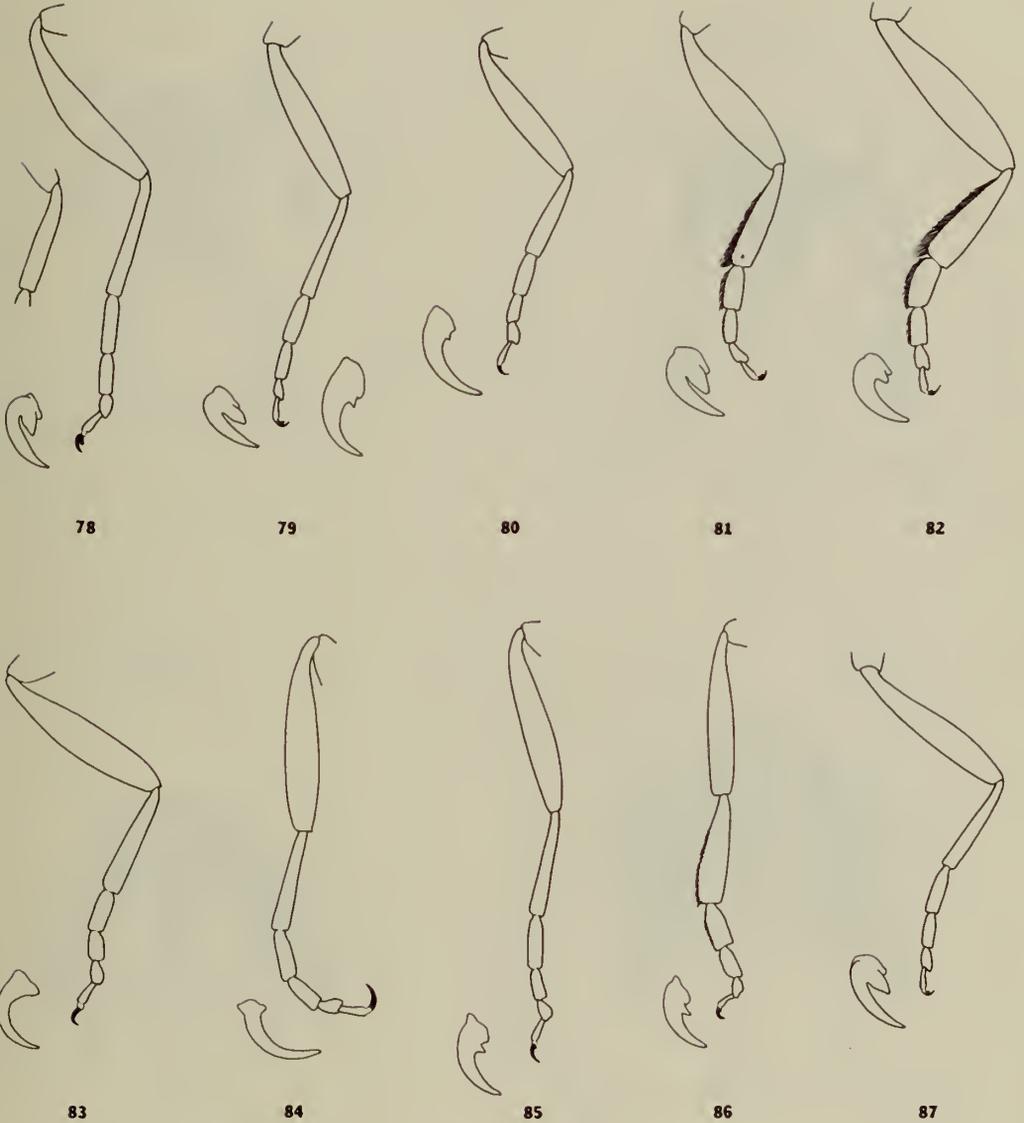
FIGS. 57-64. Form of adult head capsule in *Simulium* (left-hand figures) and in *Afrosimulium* (right-hand figures), with sex as indicated. 57-60, posterior aspect; 61-64, facial aspect, with antennae omitted.



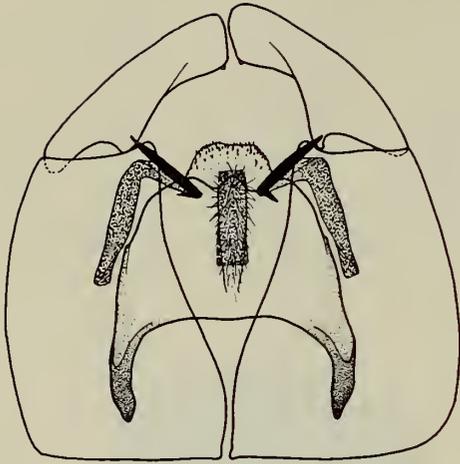
FIGS. 65-71. Adult head form in Ethiopian Simuliini. 65, usual form in profile of ♂ *Simulium* s.l. 66, usual form in profile of ♀ *Simulium* s.l. 67, form in profile of ♂ *Afrosimulium*. 68, form in profile of ♀ *Afrosimulium*. 69, profile of head and appendages of ♀ of *Simulium* (*Dexomyia*) *atlanticum* sp. n. from St. Helena. 70, head shape in dorsal view of almost all *Simulium* s.l. ♀. 71, head shape in dorsal view of ♀ of *S.* (*Dexomyia*) *atlanticum* sp. n. from St. Helena.



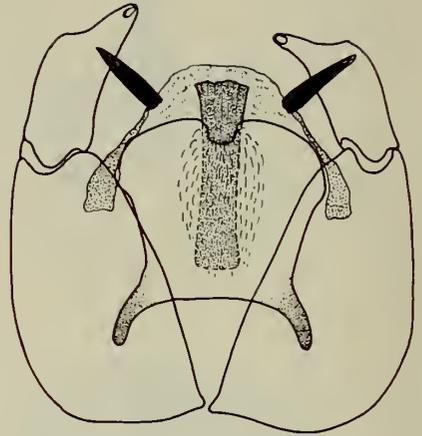
FIGS. 72-77. Scutal pattern in African *Simulium*. 72, in ♀ of subgenus *Wilhelmia*. 73, in ♀ of subgenus *Tetisimulium*. 74, in ♀ of subgenus *Odagmia*. 75, in ♂ of subgenus *Odagmia*. 76, in ♂ of bovis-group of subgenus *Metomphalus*. 77, in ♂ of a species of subgenus *Edwardsellum*. (Outline shape of the scutum has been standardized for convenience.)



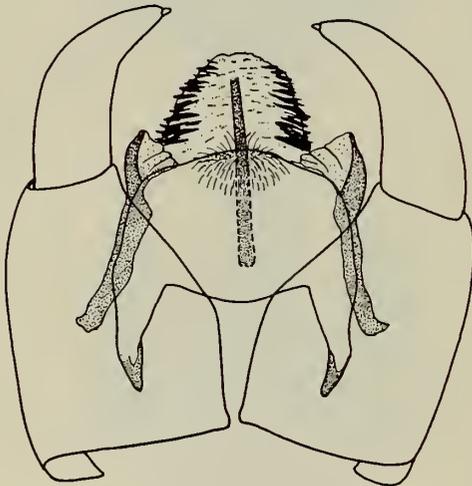
FIGS. 78-87. Fore tibia and tarsus of African subgenera of *Simulium*, with enlargement showing usual shape of the claw of the female in each subgenus. 78, *Pomeroyellum*, with two slightly different shapes of basitarsus. 79, *Eusimulium*. 80, *Lewisellum*. 81, *Phoretomyia* (species with dilated fore tarsus). 82, *Edwardsellum*. 83, *Metomphalus*. 84, *Wilhelmia*. 85, *Tetisimulium*. 86, *Odagnia*. 87, *Byssodon*.



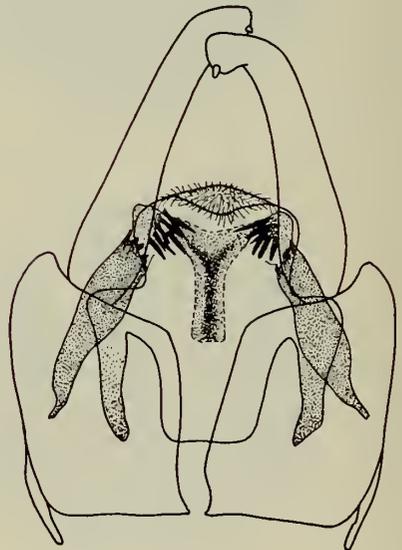
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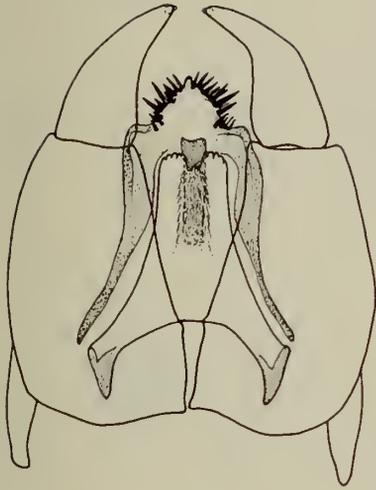


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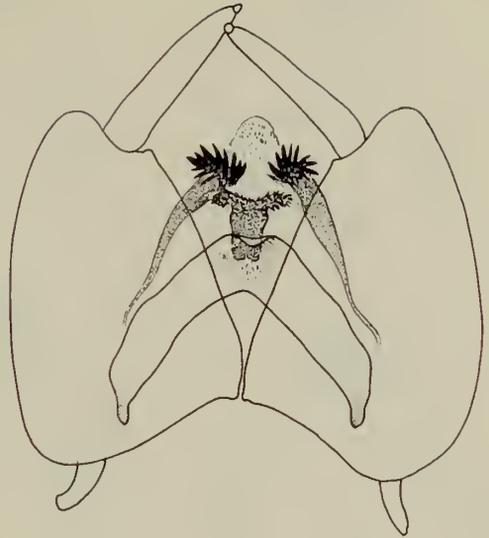


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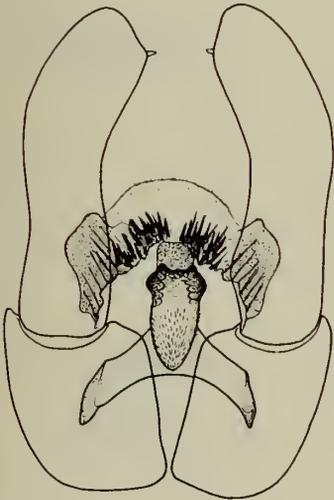
FIGS. 88-91. Usual form of ♂ hypopygium in African subgenera of *Simulium*. 88, *Eusimulium*, excluding *aureum*-group. 89, *Lewisillum*. 90, *Anasolen*. 91, *Freemanellum*.



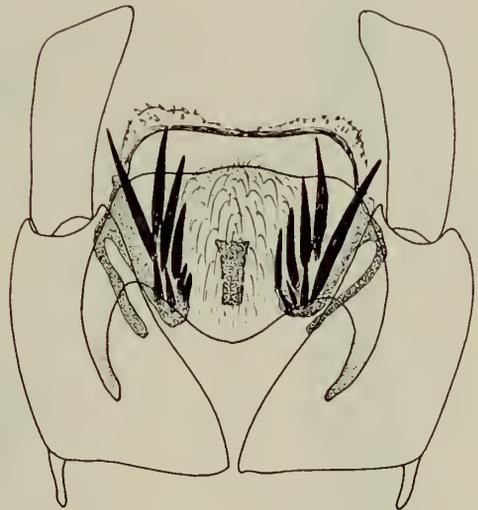
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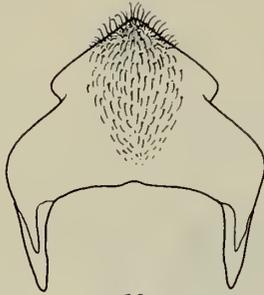


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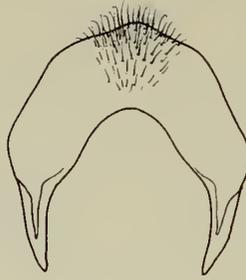


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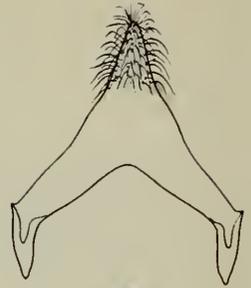
FIGS. 92-95. Usual form of ♂ hypopygium in African subgenera of *Simulium*. 92, *Metomphalus*. 93, *Wilhelmia*. 94, *Odagnia*. 95, *Byssodon*.



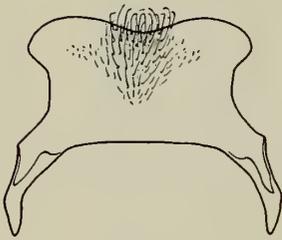
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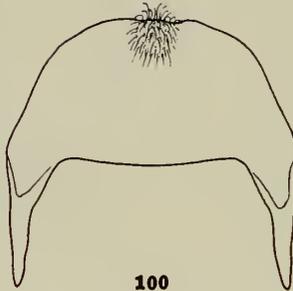
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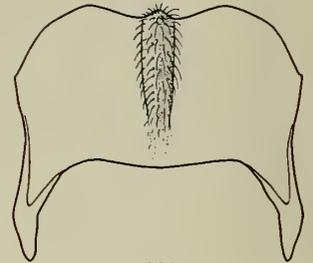
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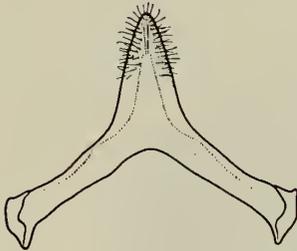
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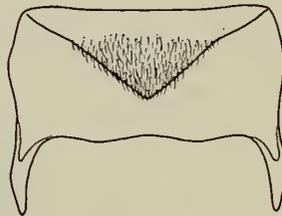
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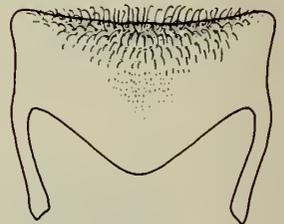
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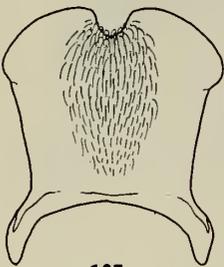
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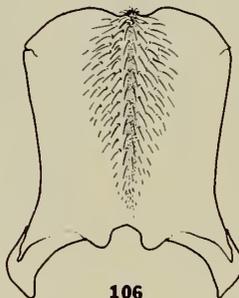
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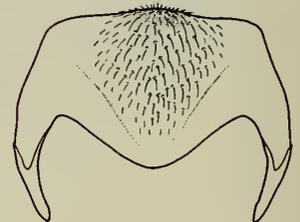
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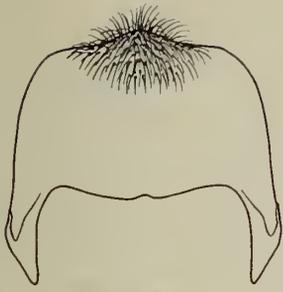


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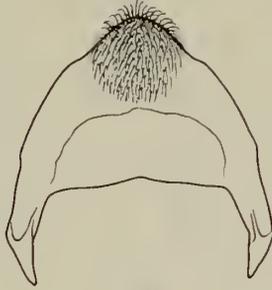


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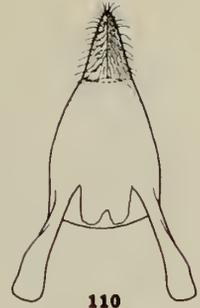
FIGS. 96-107. Form of the ventral plate of ♂ genitalia in subgenera and species-groups of African *Simulium*. 96-98, *Pomeroyellum*, *alcocki*-group. 99, *Pomeroyellum*, *cervicornutum*-group. 100, *Eusimulium*, *latipes*-group, 101, *Eusimulium*, *ruficorne*-group. 102, *Eusimulium*, *aureum*-group. 103, *Eusimulium*, *loutetense*-group. 104, *Xenosimulium*. 105, *Lewisellum*. 106, *Phoretomyia*. 107, *Byssodon*.



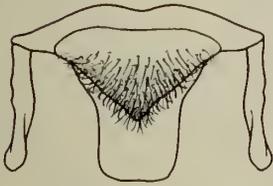
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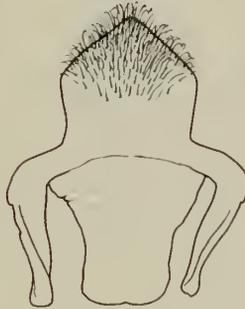
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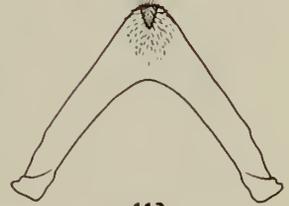
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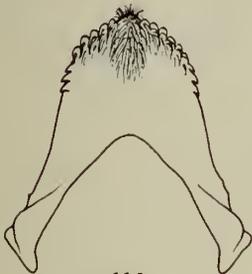
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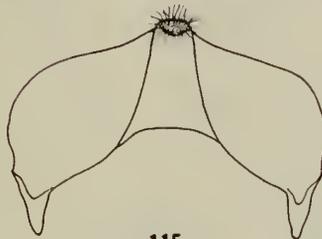
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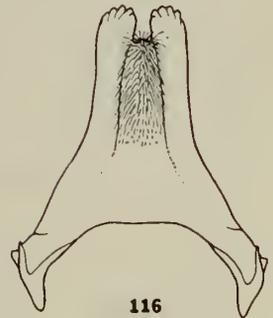
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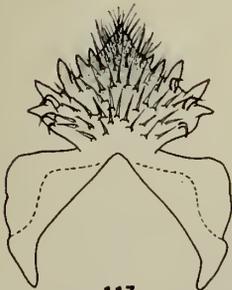
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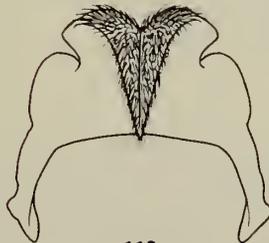
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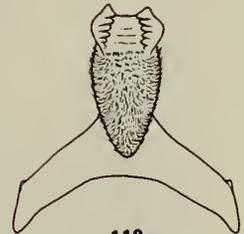
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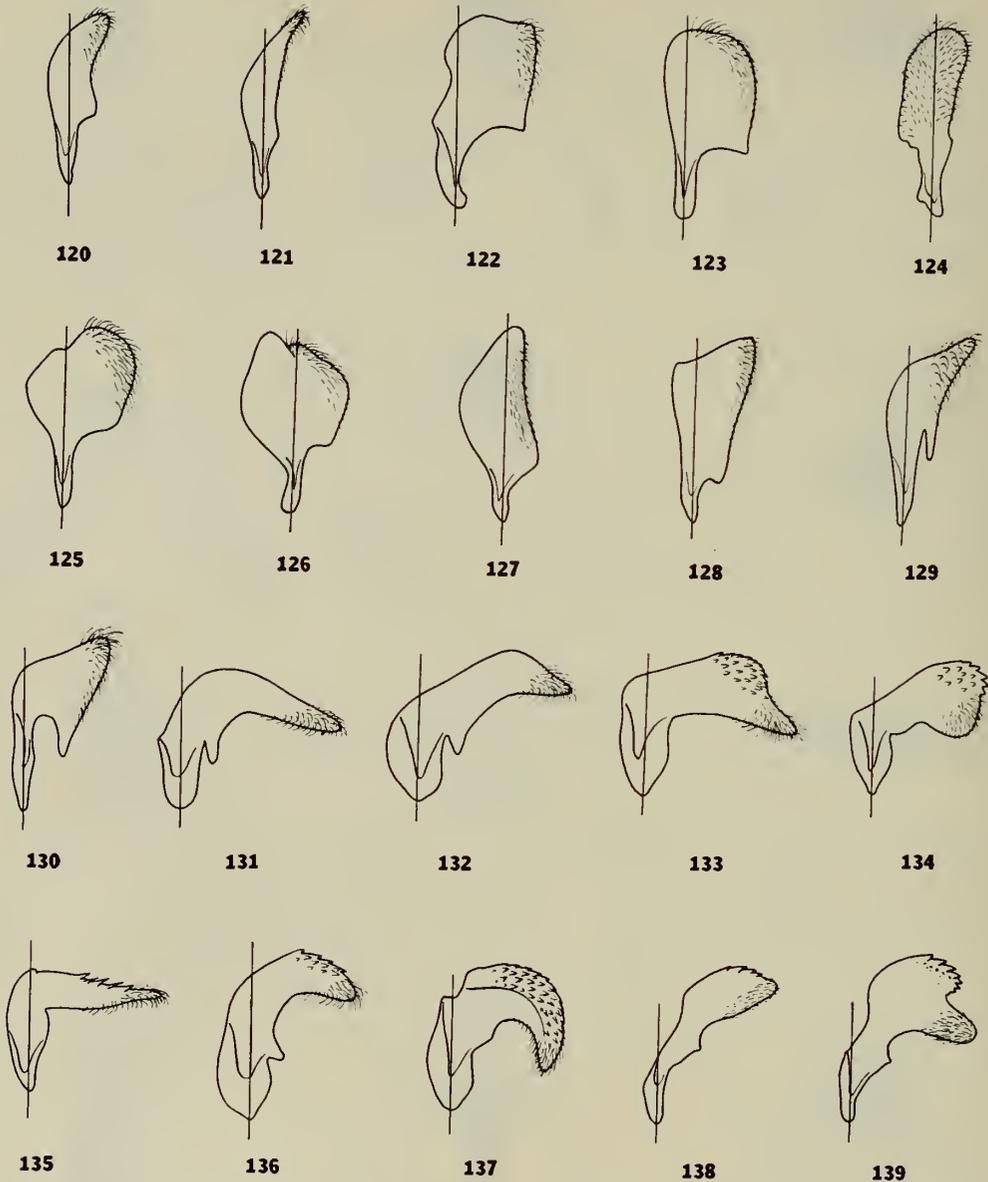


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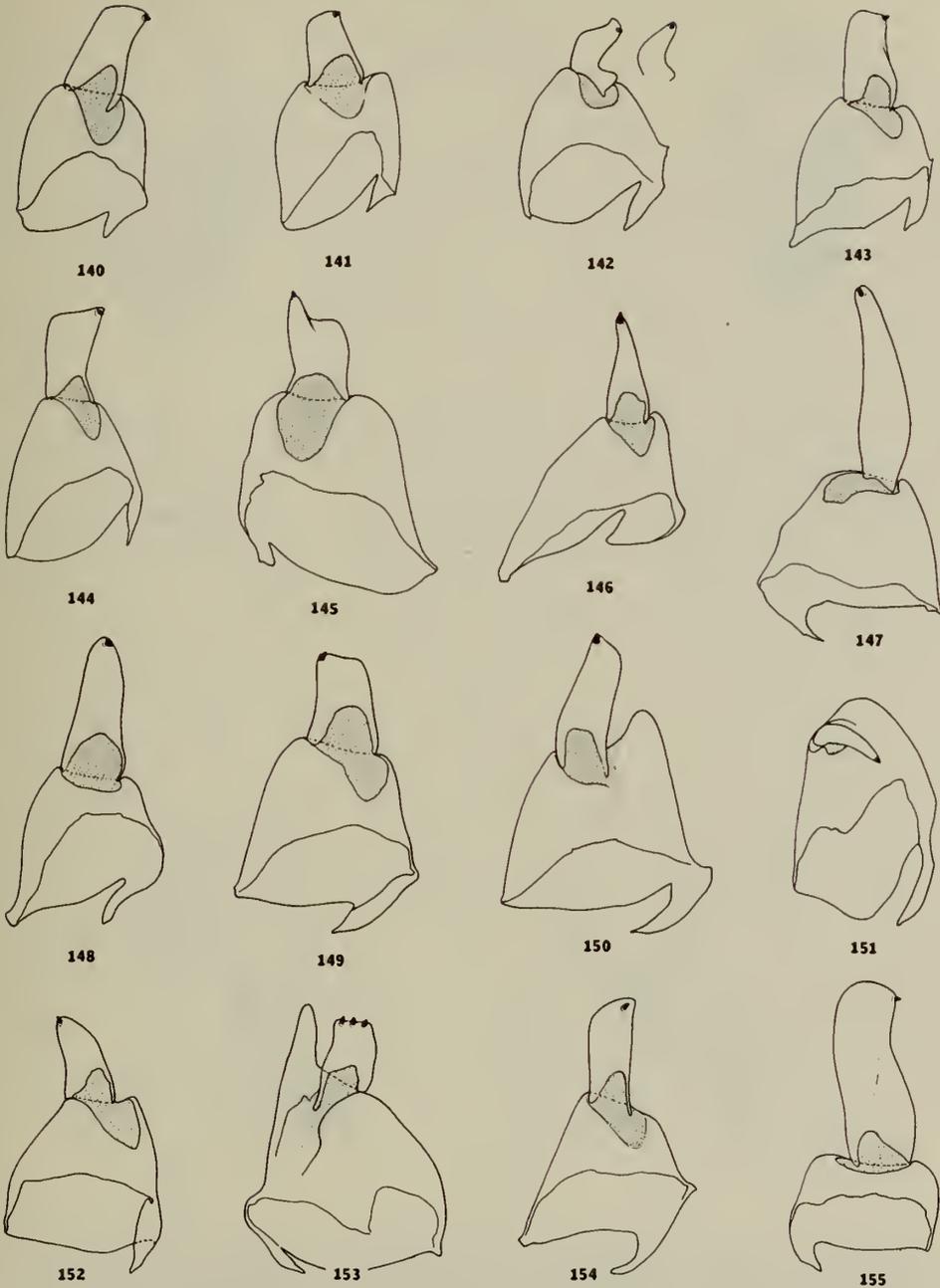


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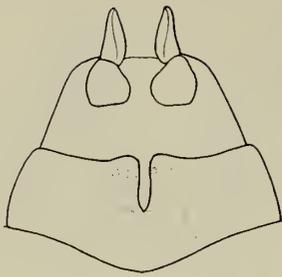
FIGS. 108-119. Form of the ventral plate of ♂ genitalia in subgenera and species-groups of African *Simulium*. 108, *Anasolen*. 109, *Anasolen*, at more tilted angle than ventral view in figure 108. 110, *Freemanellum*. 111 and 112, different views of plate in a species of *Freemanellum*. 113, *Wilhelmia*. 114 and 116, *Metomphalus*, *medusaeforme*-group. 115, *Metomphalus*, *S. wellmanni*. 117, *Metomphalus*, *albivirgulatum*-group. 118, *Edwardsellum*. 119, *Odagnia*.



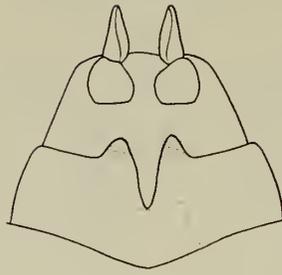
FIGS. 120-139. Showing form of ventral plate of ♂ genitalia in profile in subgenera and species-groups of African *Simulium*. 120 and 121, *Pomeroyellum*, *alcocki*-group. 122, *Pomeroyellum*, *kenyae*-group. 123, *Eusimulium*, *loutetense*-group. 124, *Eusimulium*, *aureum*-group. 125, *Eusimulium*, *ruficorne*-group. 126, *Meillonellum*. 127, *Lewisellum*. 128, *Phoretomyia*. 129, *Xenosimulium*. 130, *Byssodon*. 131, *Freemanellum*. 132, *Anasolen*. 133, *Metomphalus*, *medusaeforme*-group. 134, *Metomphalus*, *bovis*-group. 135, *Metomphalus*, *albivirgulatum*-group. 136 and 137, *Edwardsellum*. 138, *Tetisimulium*. 139, *Odagnia*.



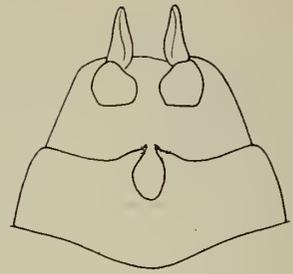
FIGS. 140-155. Form of coxite and style of ♂ genitalia in subgenera and species-groups of African *Simulium*. 140 and 141, *Pomeroyellum*. 142, *Eusimulium*, *aureum*-group. 143, and 144, *Eusimulium*, *ruficorne*-group. 145, *Lewisellum* (form similar in *Meillonellum*). 146, *Phoretomyia*. 147, *Freemanellum*. 148, *Xenosimulium*. 149, *Anasolen*. 150, *Edwardsellum*. 151, *Wilhelmia*. 152, *Metomphalus*, most forms. 153, *Metomphalus*, *S. wellmanni*. 154, *Byssodon*. 155, *Odagmia* (form similar in *Tetisimulium* and *Simulium* s. str.).



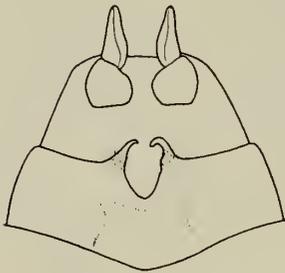
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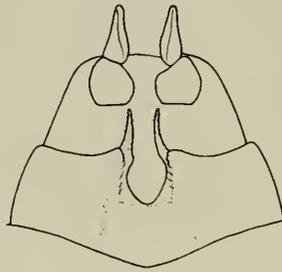
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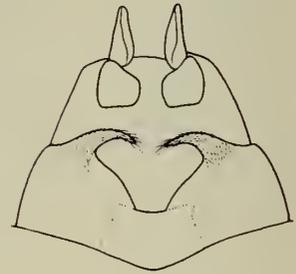
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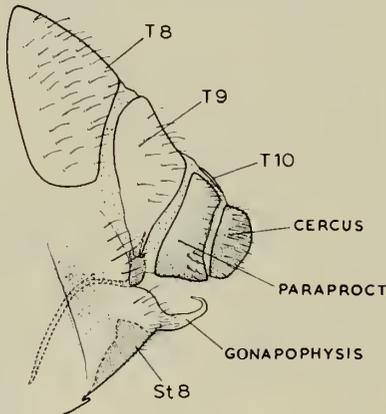
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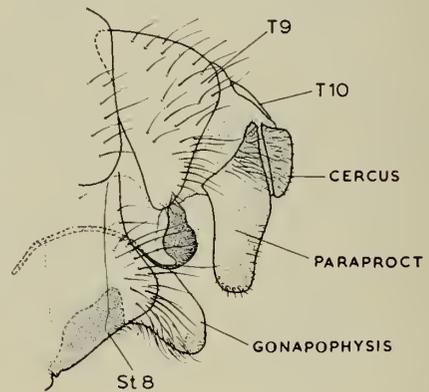
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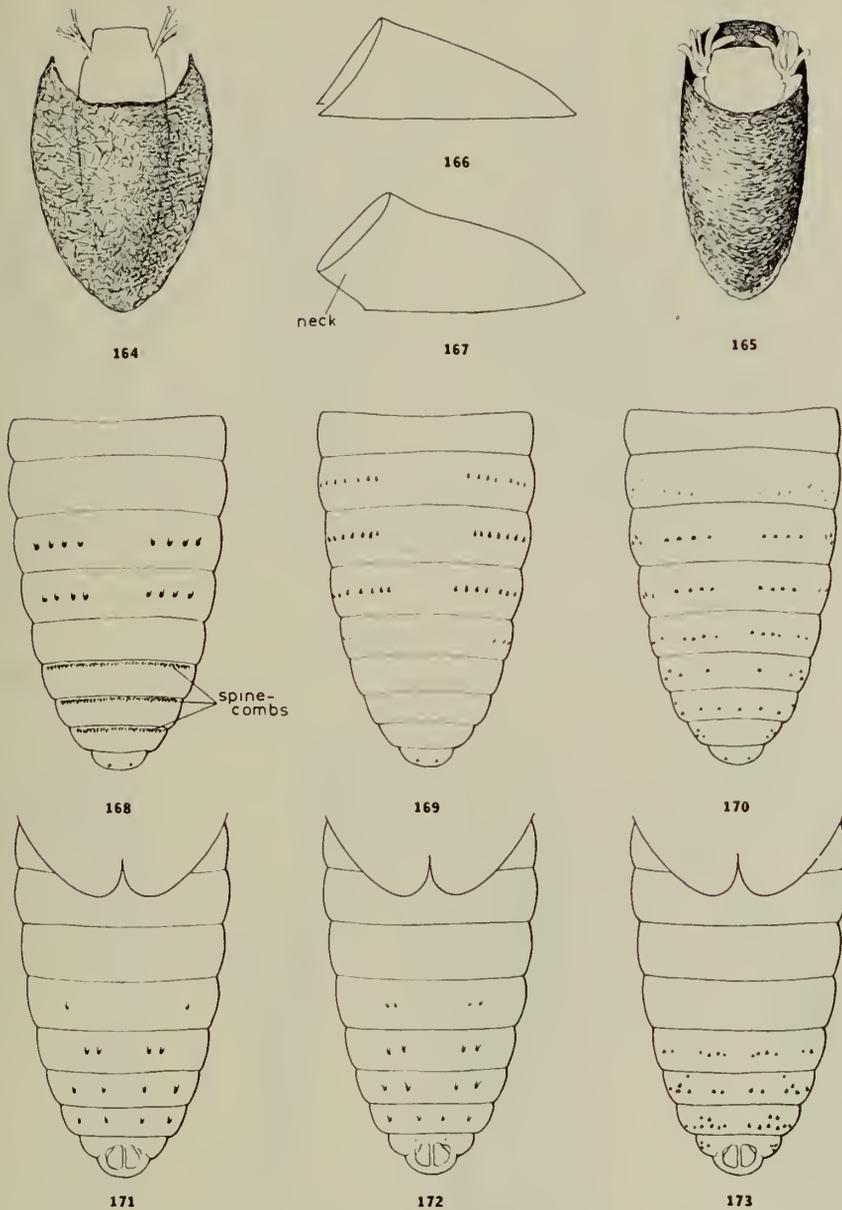


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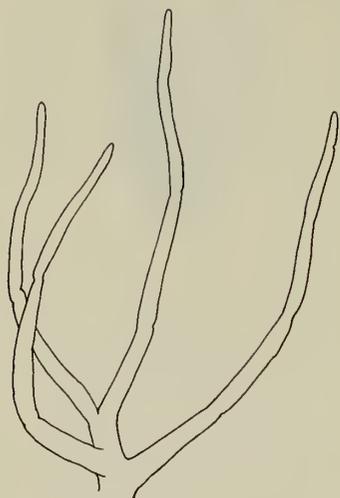


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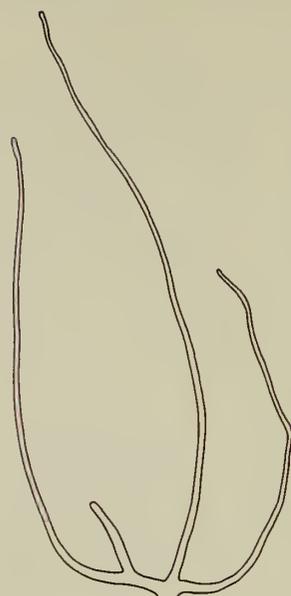
FIGS. 156-163. Female terminalia of African *Simulium*. 156-161, schematic ventral views showing form of the gonapophyses (ovipositor lobes) in : (156 and 157) subgenera *Pomeroyellum*, *Eusimulium*, *Meilloniellum*, *Lewisellum* and other subgenera with bluntly rounded gonapophyses ; (158) subgenus *Anasolen* ; (159) subgenera *Wilhelmsia*, *Metomphalus* and *Edwardsellum* with curled acuminate gonapophyses ; (160) *Metomphalus*, *S. wellmanni*. (161) subgenus *Xenosimulium* with enlarged pointed and inwardly-directed gonapophyses. 162 and 163, left lateral view of apex of ♀ abdomen showing form of cerci and paraprocts in (162) most subgenera, and in (163) forms in subgenus *Freemanellum* with enlarged paraprocts.



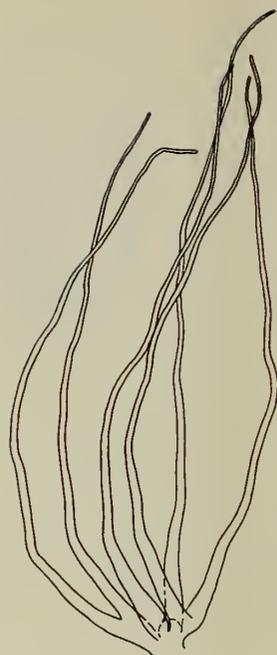
FIGS. 164-173. Form of cocoon and pupal abdomen in African *Simulium*. 164 and 165, dorsal view of (164) simple slipper-shaped cocoon, and of (165) shoe-shaped cocoon with neck. 166, outline of simple cocoon in profile. 167, outline of shoe-shaped cocoon in profile. 168-173, showing arrangement of hooks dorsally (168-170) and ventrally (171-173) on pupal abdomen in : (168 and 171) great majority of forms ; (169-173) in some phoretic forms occurring on mayflies. The spine-combs shown on the dorsum of segments 6-8 in figure 168 are absent in many forms.



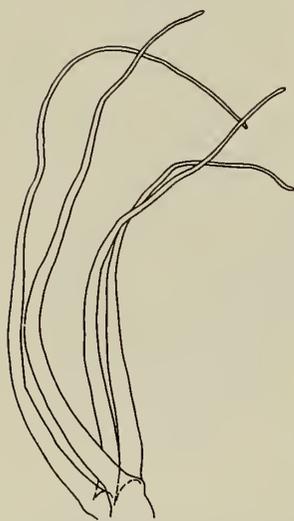
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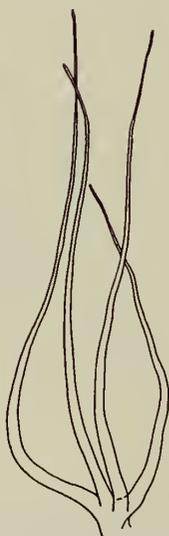
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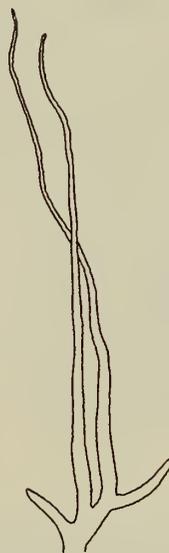
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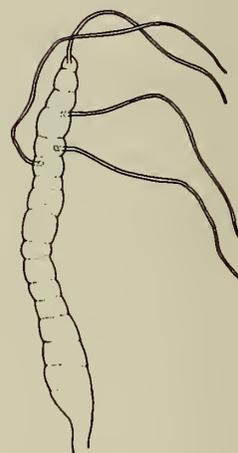
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FIGS. 174-180. Showing range of form of the pupal gill in species of the subgenus *Eusimulium* from Africa and its islands. 174, 175, 179 and 180, *ruficorne*-group. 176-178, *loutetense*-group. The gills shown in figures 175, 179 and 180 are those of species from St. Helena, the Seychelles, and Madagascar respectively. (Fig. 180 redrawn from Grenier & Grjébine (1963)).



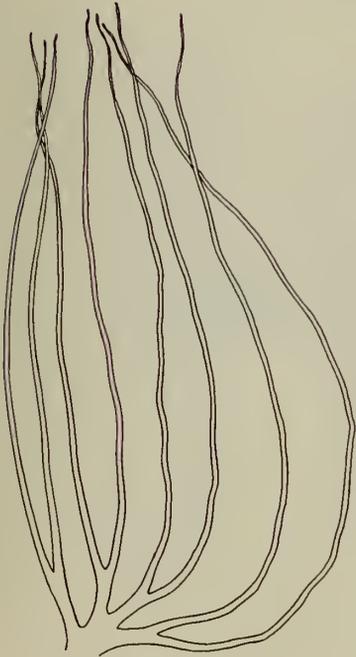
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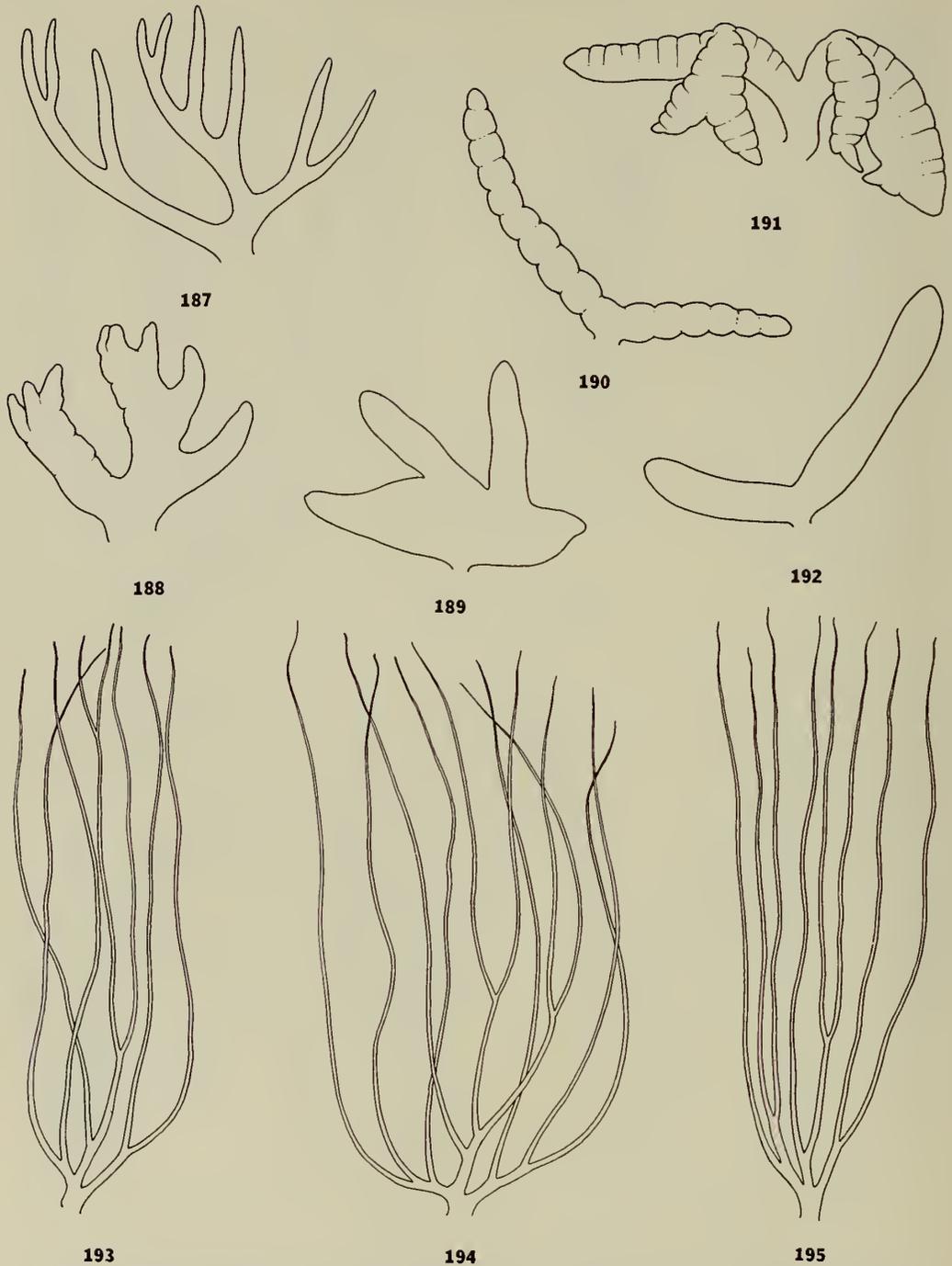


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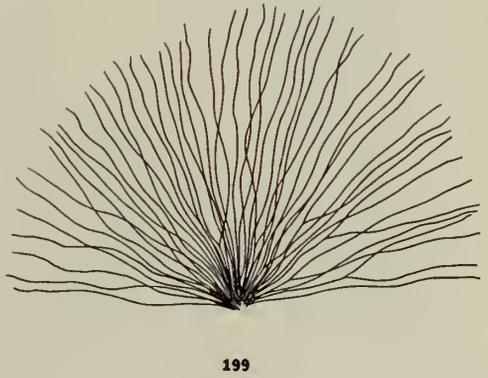
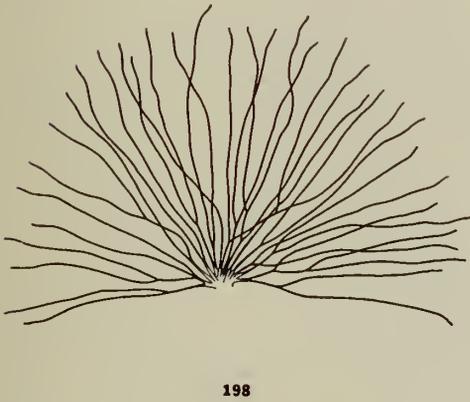
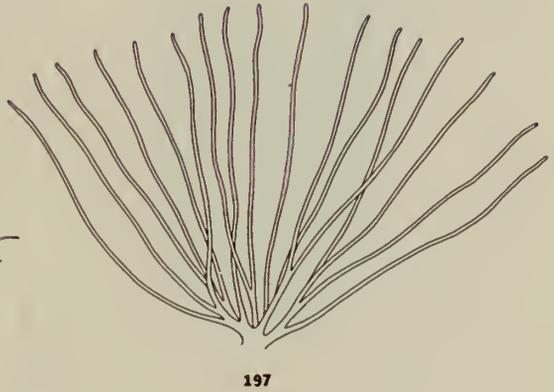
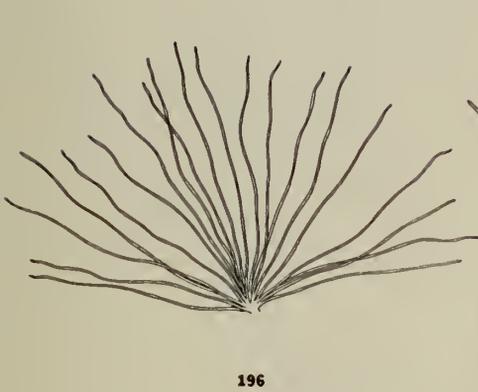


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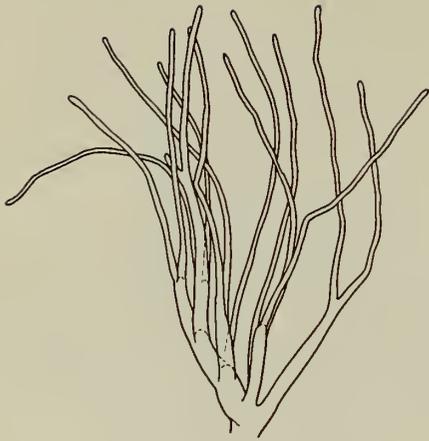
FIGS. 181-186. Pupal gill form in subgenus *Pomeroyellum*. 181, *bequaerti*-group. 182, 183 and 186, *alcocki*-group. 184, *kenyae*-group. 185, *schoutedeni*-group.



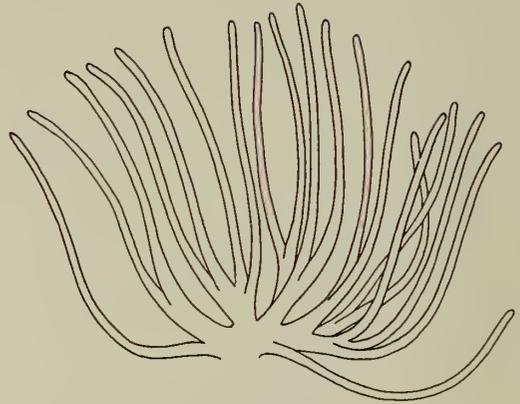
FIGS. 187-195. Pupal gill form in Ethiopian subgenera of *Simulium*. 187-192, *Pomeroyellum*, *cervicornutum*-group. 193 and 194, *Meilloniellum*. 195, *Lewisellum*. (Fig. 191 redrawn from Grenier, Germain & Mouchet (1965b)).



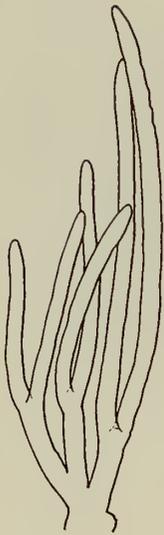
FIGS. 196-199. Pupal gill form in Ethiopian subgenera of *Simulium*. 196, *Pomeroyellum*, some *alcocki*-group. 197-199, *Phoretomyia*.



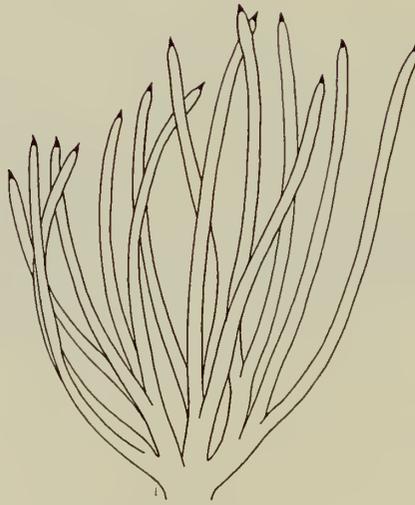
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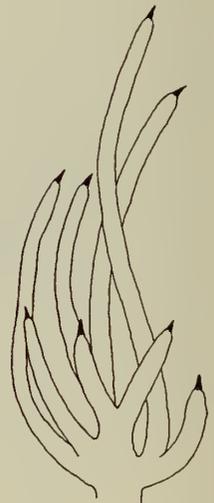
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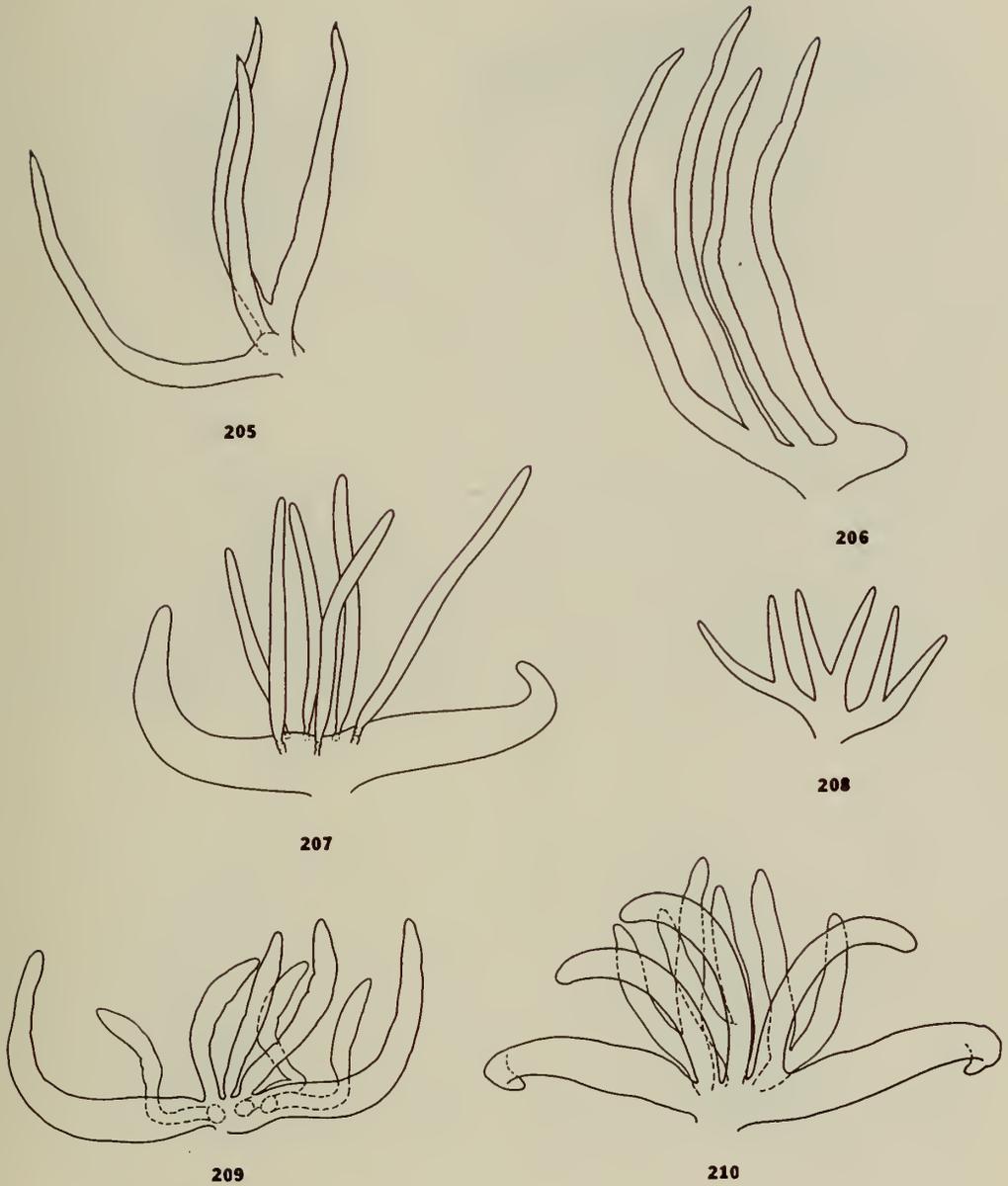


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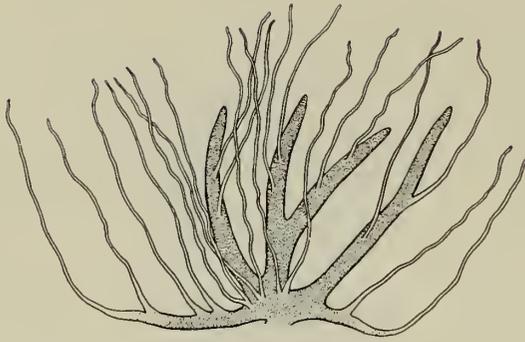


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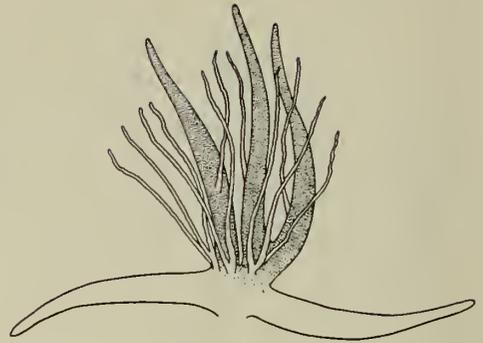
FIGS. 200-204. Pupal gill form in African subgenera of *Simulium*. 200-202, *Xenosimulium*, from Madagascar. 203 and 204, *Anasolen*.



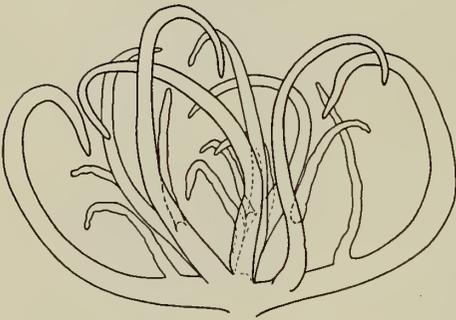
FIGS. 205-210. Pupal gill form in African subgenera of *Simulium*. 205 and 206, *Freemanellum*. 207, *Wilhelmia*. 208, *S. gyas*, doubtfully assignable to subgenus *Metomphalus*. 209 and 210, *Edwardsellum*.



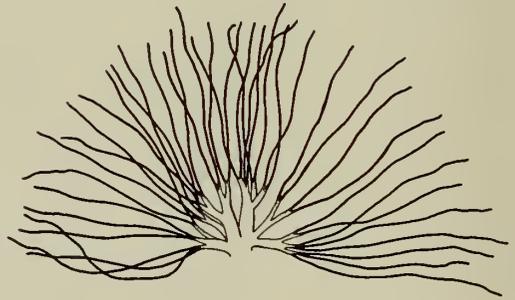
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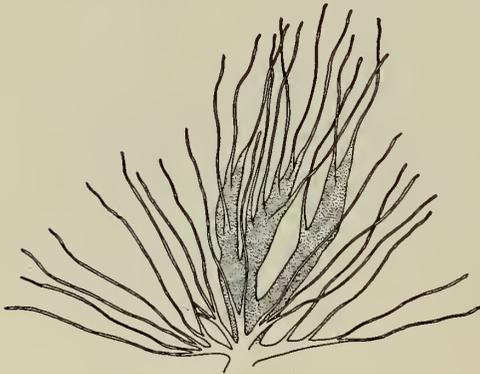
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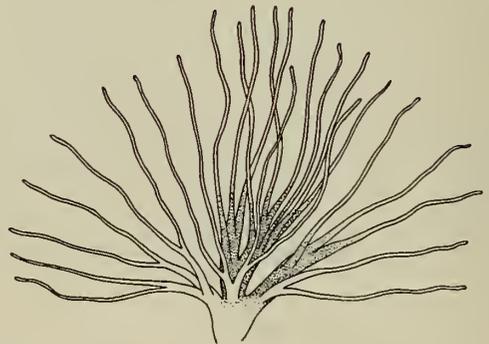
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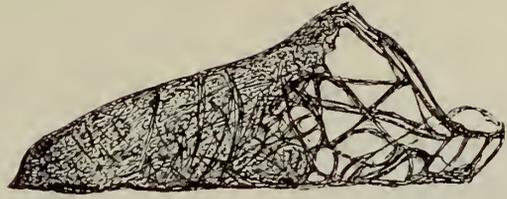


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FIGS. 211-216. Pupal gill form in subgenus *Metomphalus*. 211-213, *medusaeforme*-group. 214, *albivirgulatum*-group. 215 and 216, *bovis*-group.



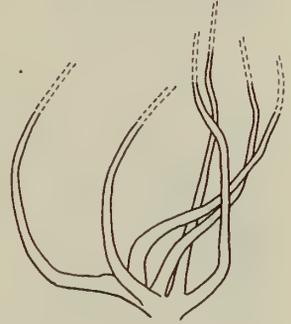
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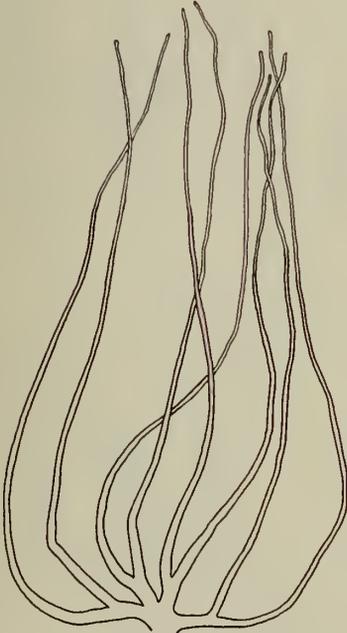
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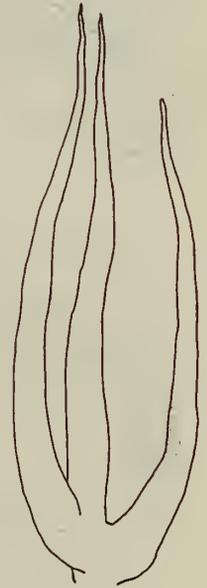
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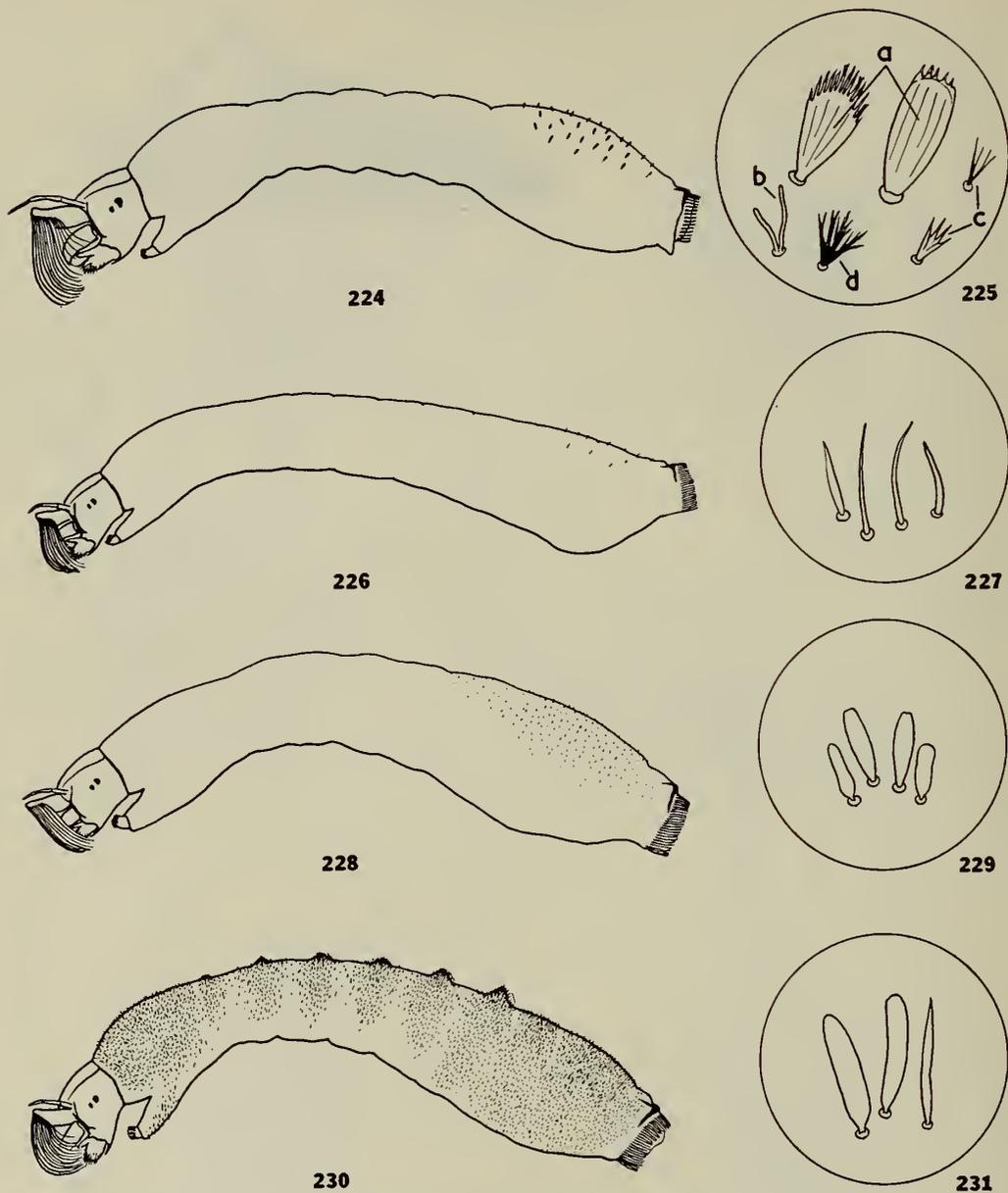


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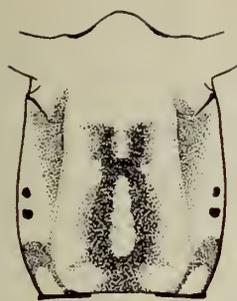


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FIGS. 217-223. Pupal characters of African Simuliini. 217, gill form in subgenus *Tetisimulium*. 218, side view of cocoon in subgenus *Tetisimulium*. 219, gill form in subgenus *Simulium* s. str. from North Africa. 220, gill form in subgenus *Odagnia*. 221 and 222, gill form in subgenus *Byssodon*. 223, gill form in genus *Afrosimulium*.



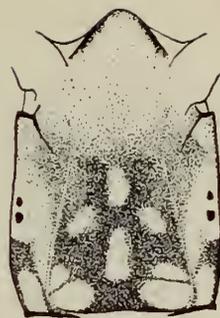
FIGS. 224-231. Larval body form and cuticular ornamentation in African *Simulium*. 224, body shape in forms with ventral papillae. 225, types of seta or scale often associated with body form shown in fig. 224. 226, body-shape in most forms without ventral papillae, drawn from *medusaeforme*-group of *Metomphalus*. 227, simple setae sometimes associated with body form shown in fig. 226. 228, body shape in *bovis*-group of *Metomphalus*. 229, truncate scales associated with body form of *bovis*-group (228). 230, body form in subgenus *Edwardsellum* showing dorsal abdominal tubercles and dense covering of scales. 231, types of scale associated with body form of *Edwardsellum* (230). For explanation of lettering a-d in Text-fig. 225 see text.



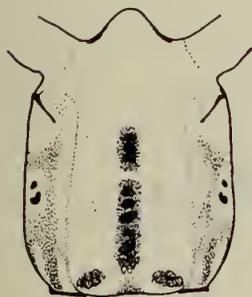
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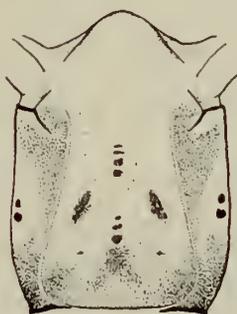
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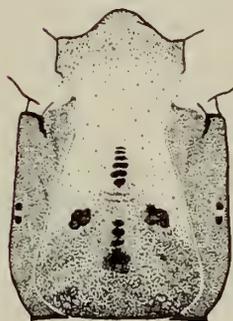
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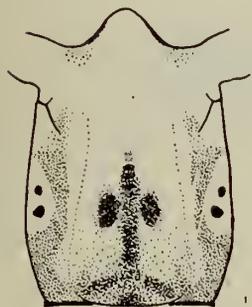
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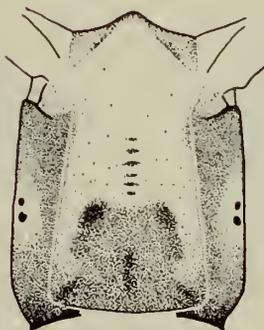
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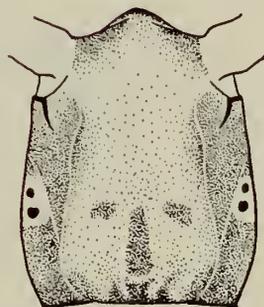
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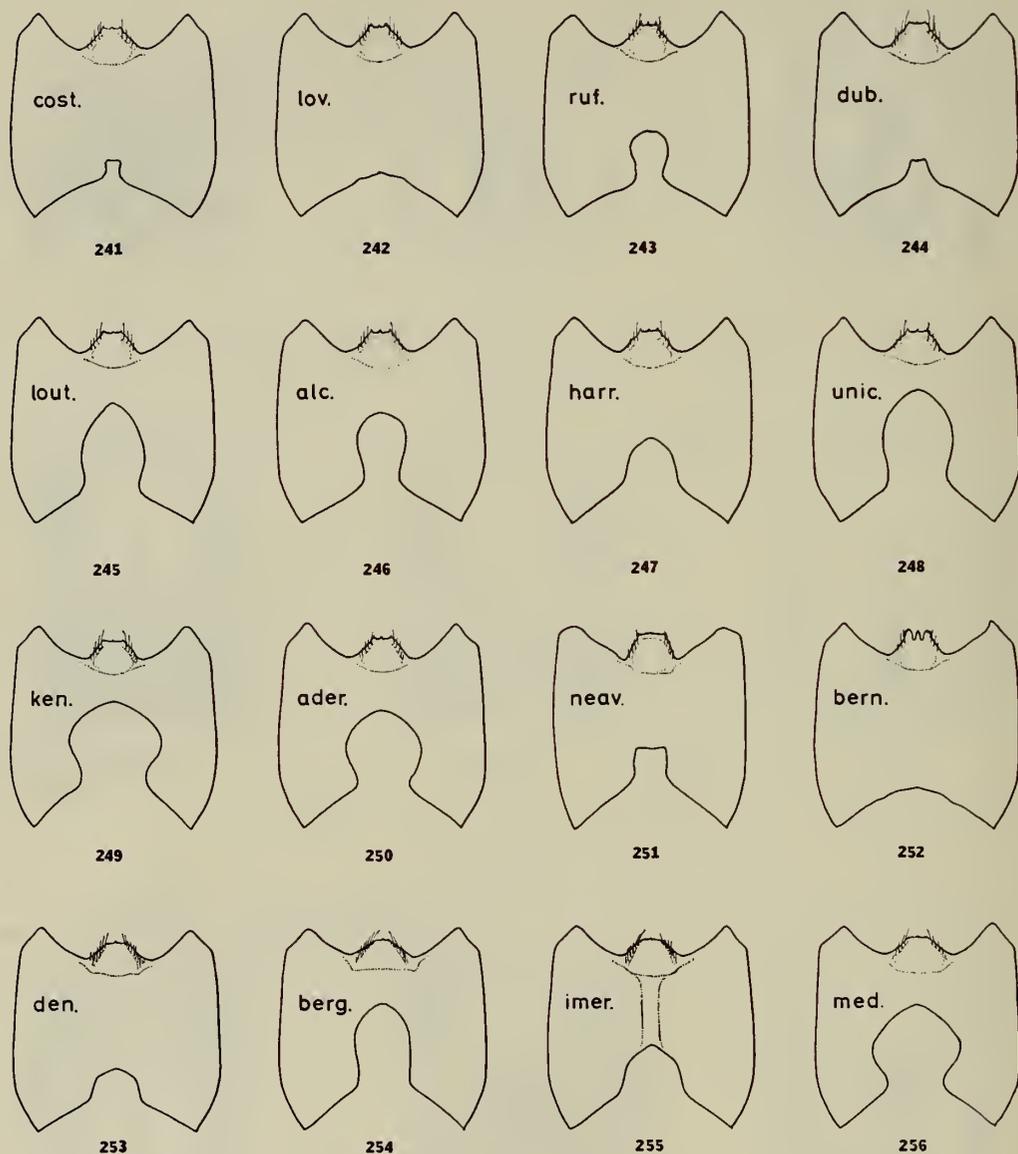


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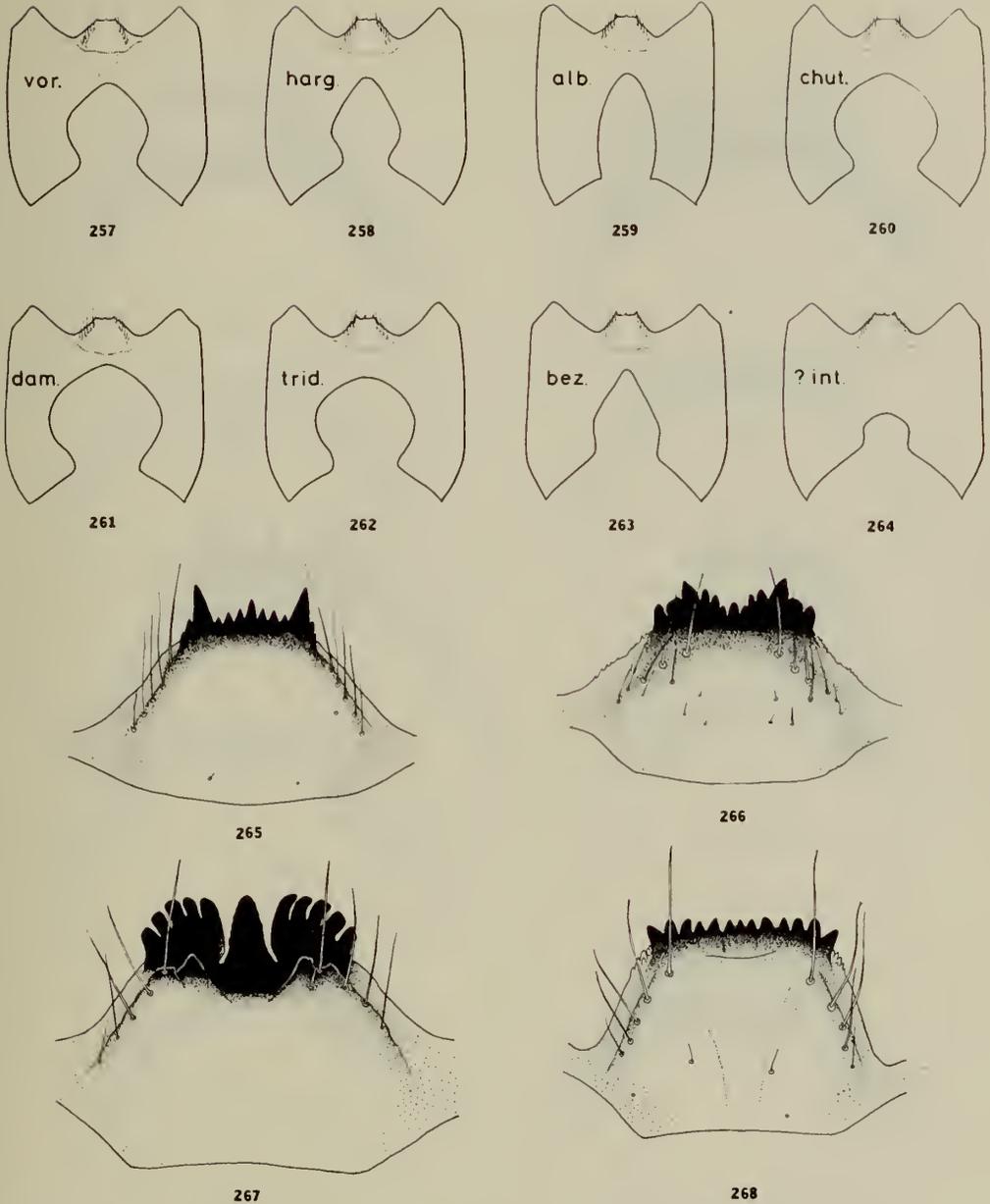


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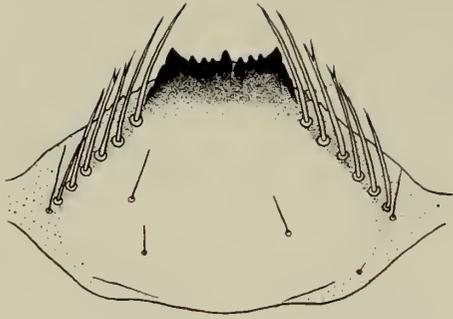
FIGS. 232-240. Dorsal head pattern in larvae of African *Simulium* (232-234 showing forms with negative head-spots and 235-240 showing forms with positive head-spots). 232 and 234, subgenus *Pomeroyellum*. 233, subgenus *Meilloniellum*. 235 and 236, subgenus *Eusimulium*. 237, subgenus *Anasolen*. 238 and 239, *medusaeforme*-group of subgenus *Metomphalus*. 240, subgenus *Edwardsellum*.



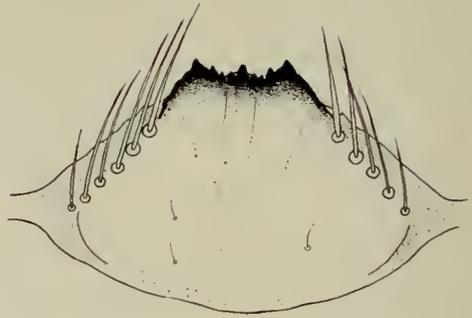
FIGS. 241-256. Outline ventral views of shape of larval head capsule in African *Simulium* showing range of form of postgenal cleft in subgenera and species-groups. 241, *Eusimulium*, *latipes*-group. 242-244, *Eusimulium*, *ruficorne*-group. 245, *Eusimulium*, *loutense*-group. 246, *Pomeroyellum*, *alcocki*-group. 247, *Pomeroyellum*, *bequaerti*-group. 248, *Pomeroyellum*, *cervicornutum*-group. 249, *Pomeroyellum*, *kenyae*-group. 250, *Meilioniellum*. 251, *Lewisellum*. 252, *Phoretomyia*. 253, *Anasolen*. 254, *Freemanellum*. 255, *Xenosimulium*. 256, *Wilhelmina*.



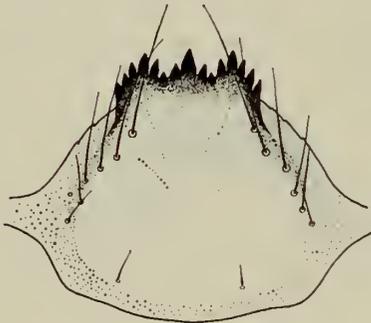
FIGS. 257-268. Form of the postgenal cleft (257-264) and of the hypostomium (265-268) in mature larvae of African *Simulium*. 257 and 258, *Metomphalus*, *medusaeforme*-group. 259, *Metomphalus*, *albivirgulatum*-group. 260, *Metomphalus*, *bovis*-group. 261, *Edwardsellum*. 262, *Byssodon*. 263, *Tetisimulium*. 264, *Odagmia*. 265, *Phoretomyia*, *lumbwanum*-group. 266, *Phoretomyia*, *copleyi*-group. 267, *Phoretomyia*, *berneri*-group. 268, *Lewisellum*. (Figures 265-268 illustrate the hypostomium in phoretic forms.)



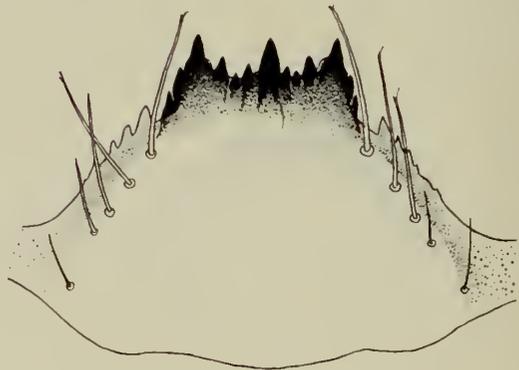
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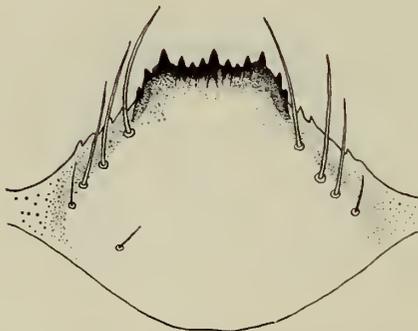
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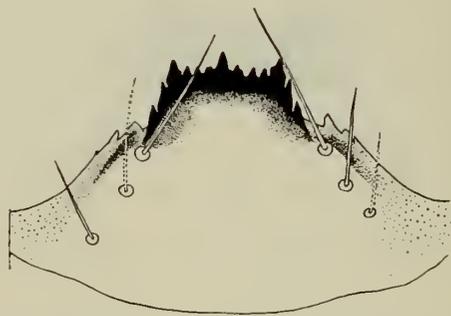
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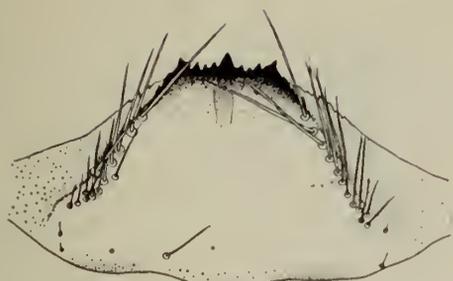


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FIGS. 269-274. Form of the larval hypostomium in subgenera of African *Simulium*.  
269-272, *Eusimulium*. 273, *Pomeroyellum*. 274, *Byssodon*.



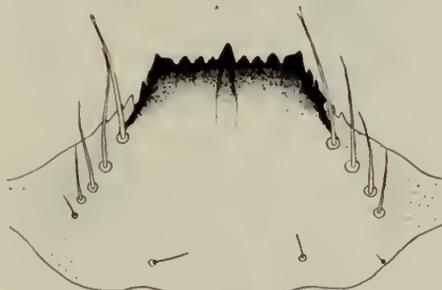
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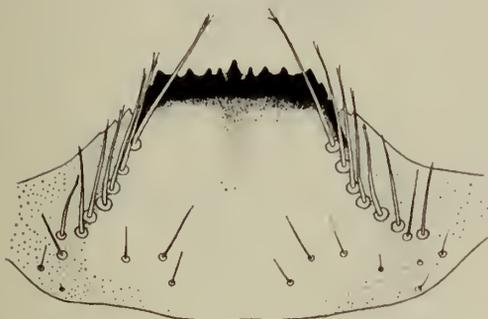
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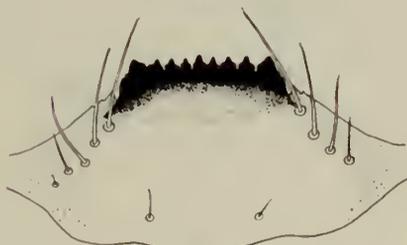
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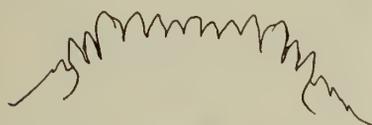
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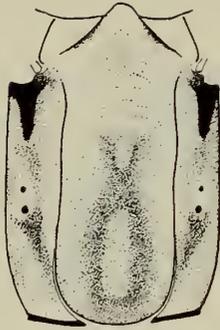


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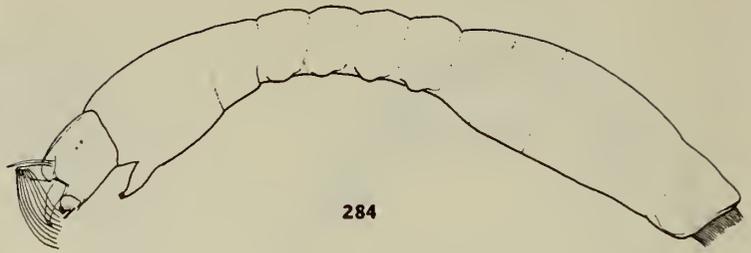


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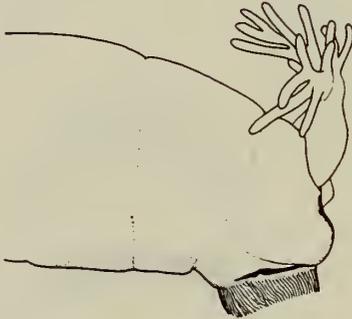
FIGS. 275-282. Form of the larval hypostomium in subgenera and species-groups of African *Simulium*. 275, *Anasolen*. 276, *Freemanellum*. 277, *Xenosimulium*. 278 and 279, *Metomphalus*, *medusaeforme*-group. 280, *Metomphalus*, *bovis*-group. 281, *Metomphalus*, *albivirgulatum*-group, shape of apical teeth only. 282, *Edwardsellum*.



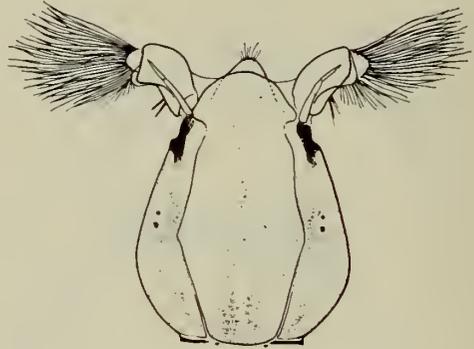
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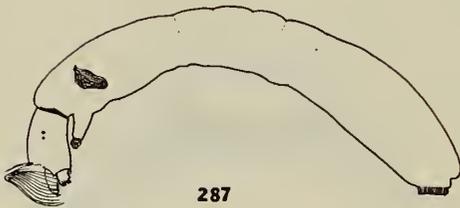
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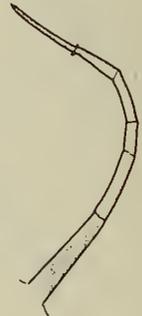
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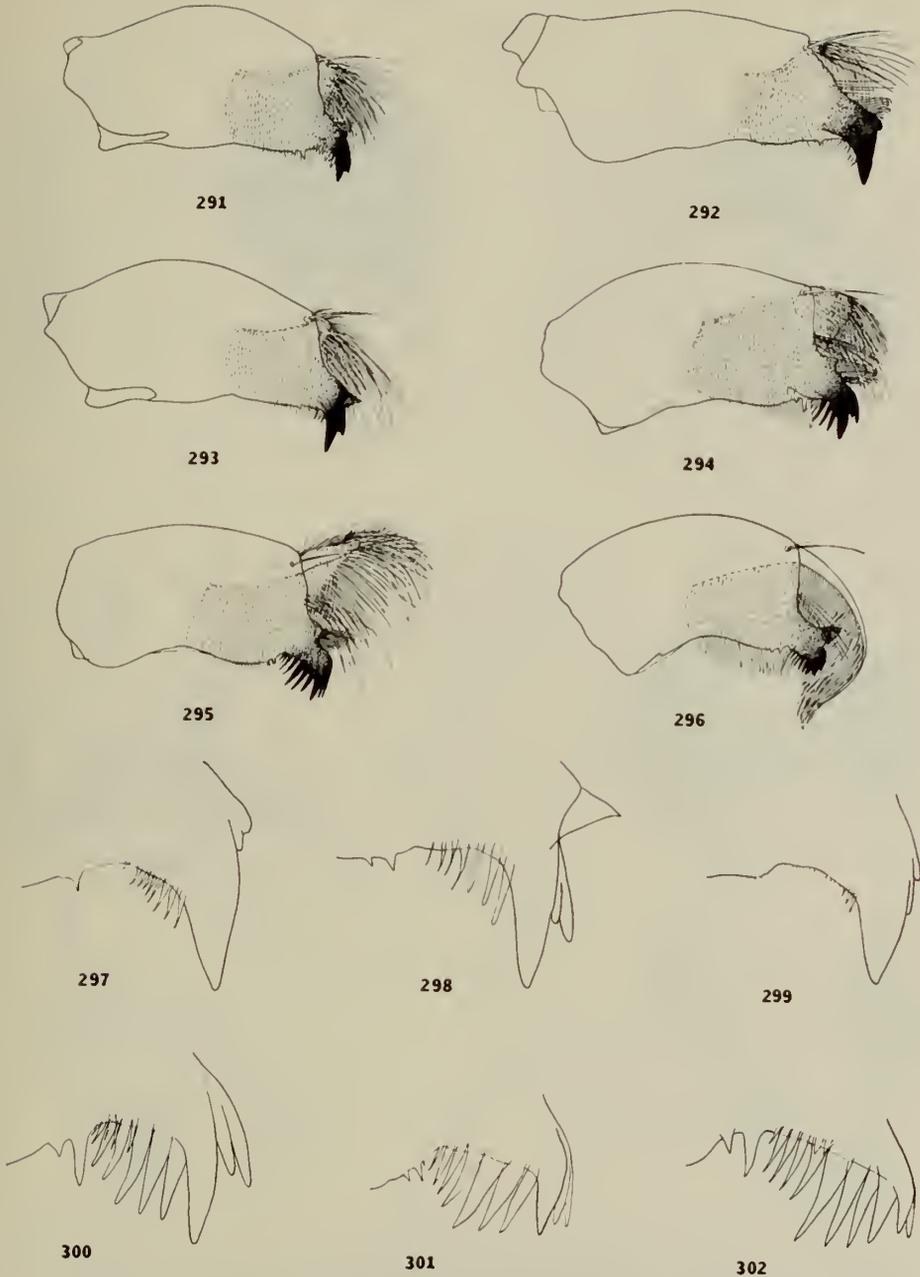


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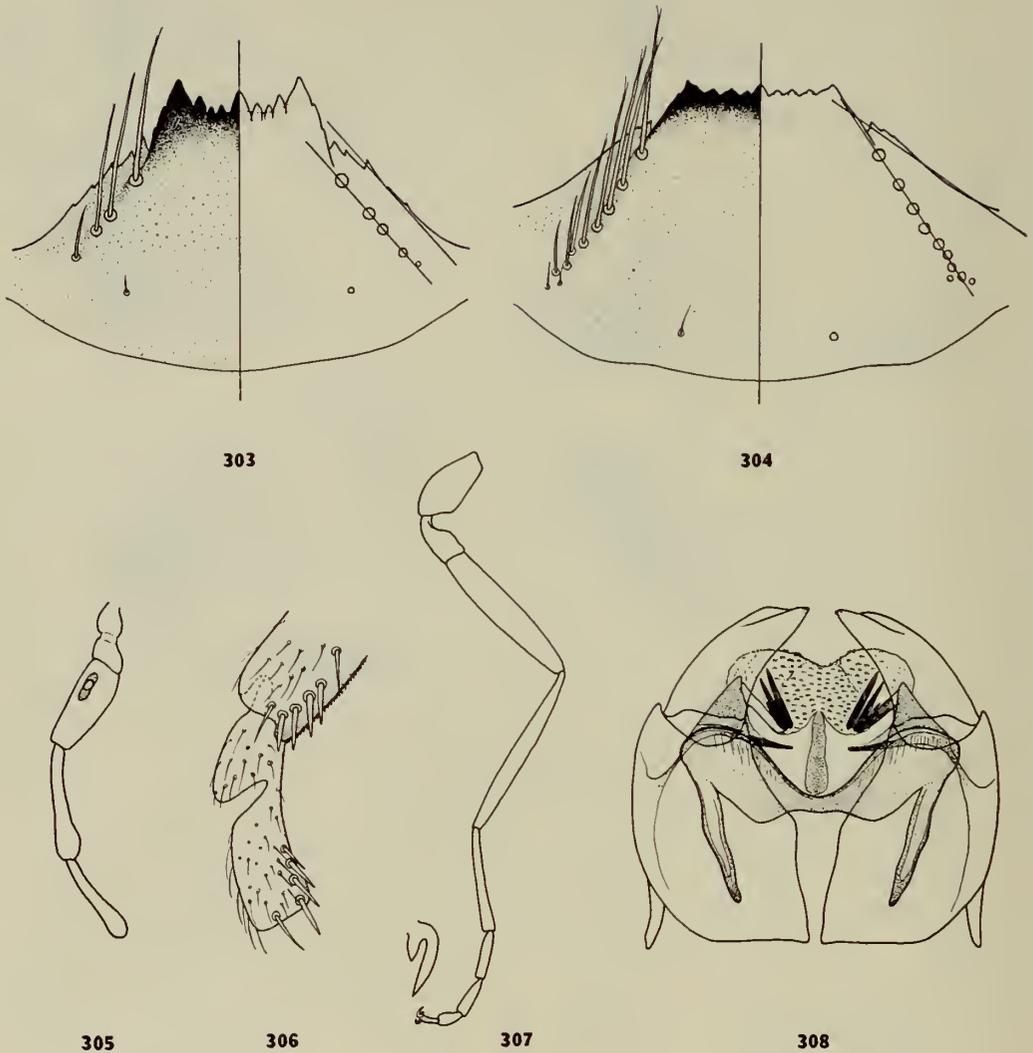


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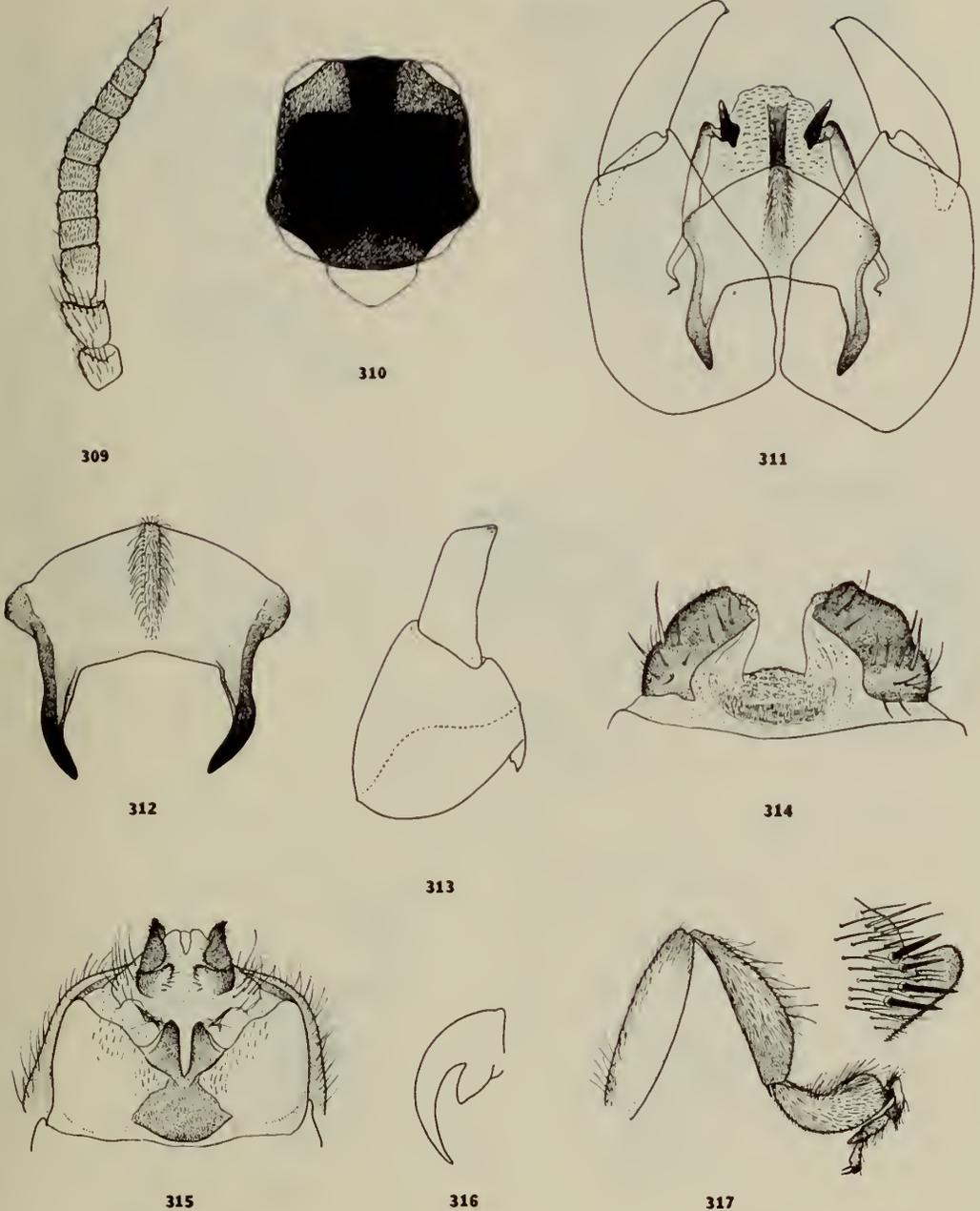
FIGS. 283–290. Larval characters of African *Simulium*. 283, dorsal view of head in subgenus *Lewisellum* showing shape of cephalic apotome and negative pattern. 284, body shape in profile in subgenus *Lewisellum*. 285, apex of abdomen in subgenus *Phoretomyia* showing ventral orientation of posterior cercus. 286, dorsal view of head in *copleyi*-group of subgenus *Phoretomyia* showing straight 'cut-off' cephalic fans. 287, profile of unusual body shape in *albivirgulatum*-group of *Metomphalus*. 288, antenna of forms with short third segment. 289, antenna of forms with long slender third segment. 290, antenna in subgenus *Xenosimulium*, showing secondary annulation.



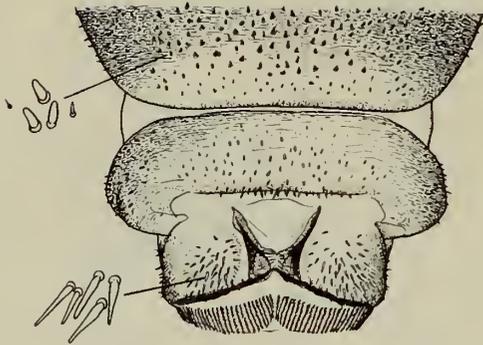
FIGS. 291-302. Larval mandible of African *Simulium*; inner aspect of entire mandible (291-296) and apical teeth only (297-302). 291, general form in subgenera *Pomeroyellum*, *Eusimulium* and *Meilloniellum*. 292, *Lewisellum*. 293, *Phoretomyia*, *lumbwanum*-group. 294, form in subgenera *Metomphalus* and *Edwardsellum*. 295, *Fremanellum*. 296, *Xenosimulium*. 297, *Lewisellum*. 298, *Phoretomyia*, *lumbwanum*-group. 299, *Phoretomyia*, *copleyi*-group. 300, *Metomphalus* and *Edwardsellum*. 301, *Fremanellum*. 302, *Xenosimulium*.



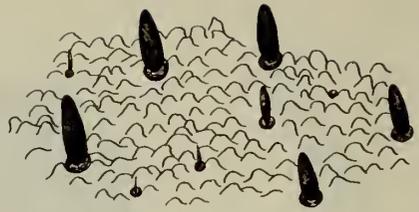
FIGS. 303-308. Showing characters of the larval hypostomium in genus *Simulium* (303 and 304) and characters of the genus *Afrosimulium* (305-308). 303, form of hypostomium in subgenera in which rows of hypostomial setae lie parallel with lateral margins of hypostomium. 304, form of hypostomium in subgenera in which rows of hypostomial setae conspicuously diverge posteriorly from lateral margins of hypostomium. 305, maxillary palp (♀) in *Afrosimulium*. 306, second hind tarsal segment and apex of hind basitarsus in *Afrosimulium*, showing deep pedisulcus and very reduced calcipala. 307, fore leg of *Afrosimulium*, and tarsal claw of female. 308, ♂ hypopygium of *Afrosimulium*.



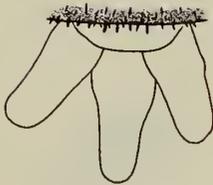
FIGS. 309-317. *Simulium (Dexomyia) atlanticum* sp. n., characters of the adult. 309, antenna. 310, scutum of ♂. 311, ♂ genitalia, ventral view after clearance. 312, ventral plate of ♂ genitalia. 313, coxite and style of ♂ genitalia. 314, cerci of ♂. 315, terminalia of ♀ in ventral view. 316, tarsal claw of ♀. 317, hind leg of ♂ with enlargement of calcipala.



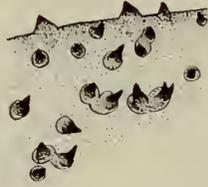
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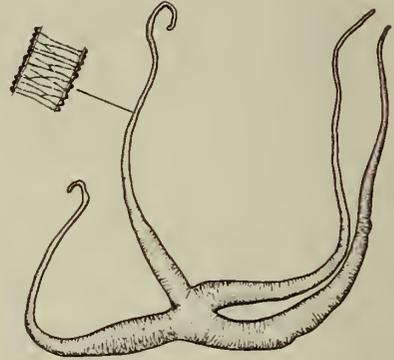
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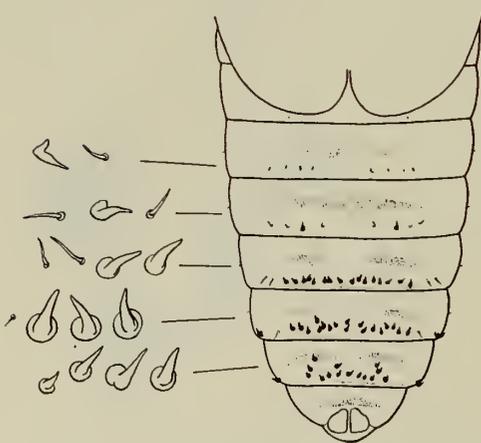
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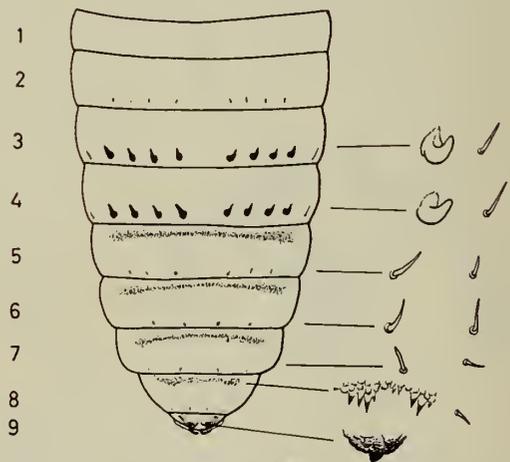
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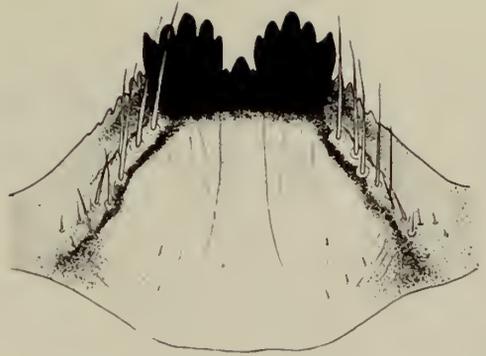


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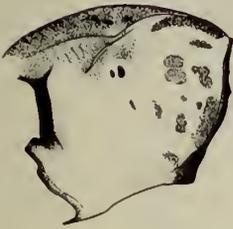
FIGS. 318-324. *Simulium (Dexomyia) atlanticum* sp. n., characters of the larva and pupa. 318, end of larval abdomen in dorsal view, with enlargement showing setae and spinules. 319, showing spinules and rugose surface of larval abdominal cuticle. 320, rectal gills of larva. 321, thorn-like tubercles of pupal thorax. 322, pupal gill, with enlargement of sculpture. 323 and 324, ventral (323) and dorsal (324) views of pupal abdomen with enlargements of cuticular armature on the segments indicated.



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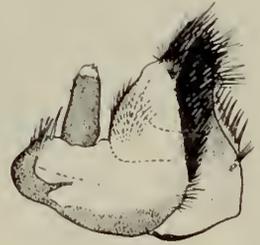
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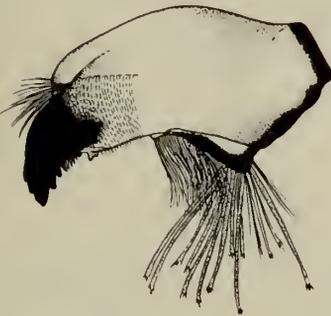
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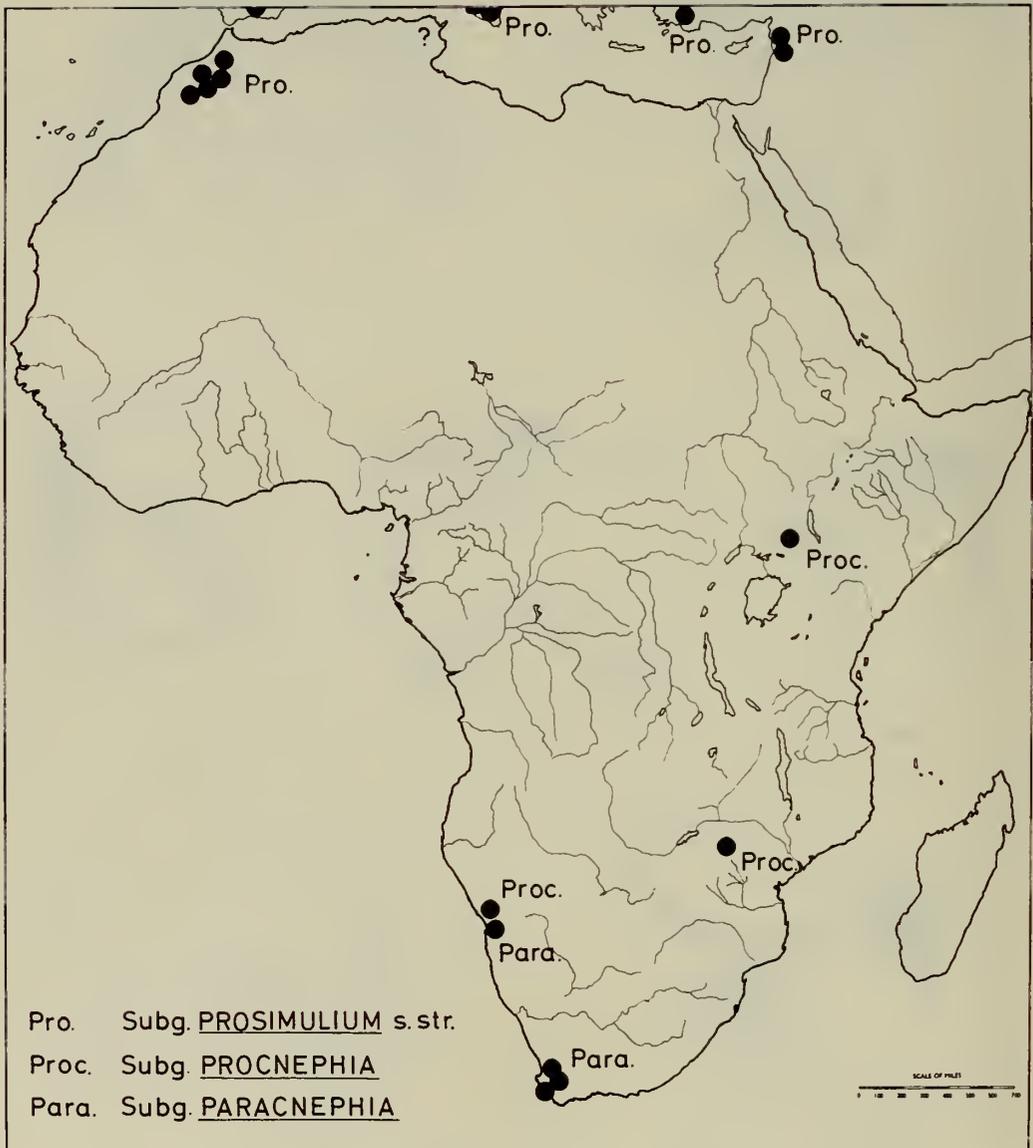


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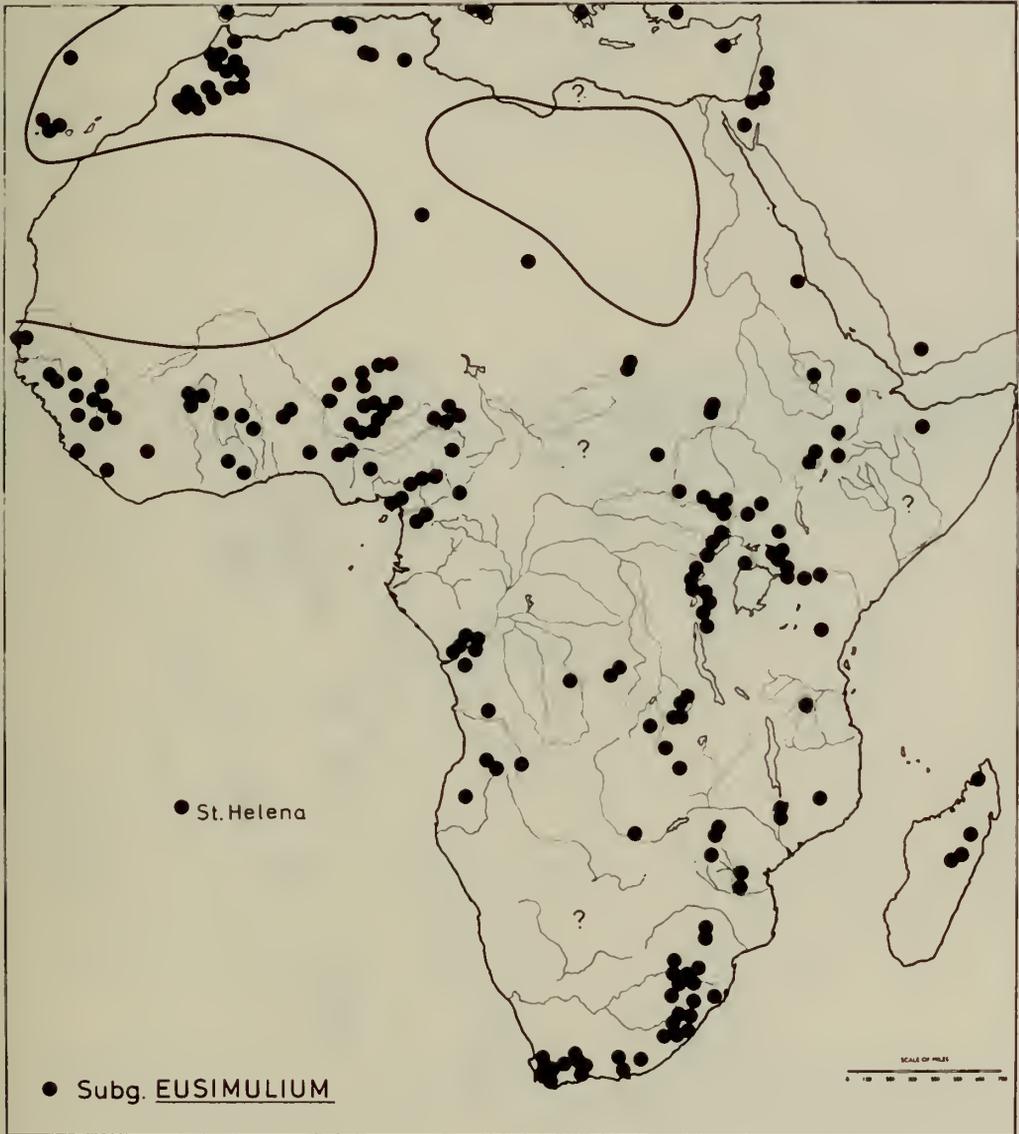


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FIGS. 325-331. *Simulium (Dexomyia) atlanticum* sp. n., characters of the larva. 325, head in dorsal view, showing remarkable thickened rays of cephalic fan, pigmentation and shape of cephalic apotome. 326, hypostomium. 327, side view of head capsule and its pigmentation. 328, ventral view of head capsule showing pigmentation and shape of post-genal cleft. 329, maxilla. 330, mandible. 331, shape of apical mandibular teeth.



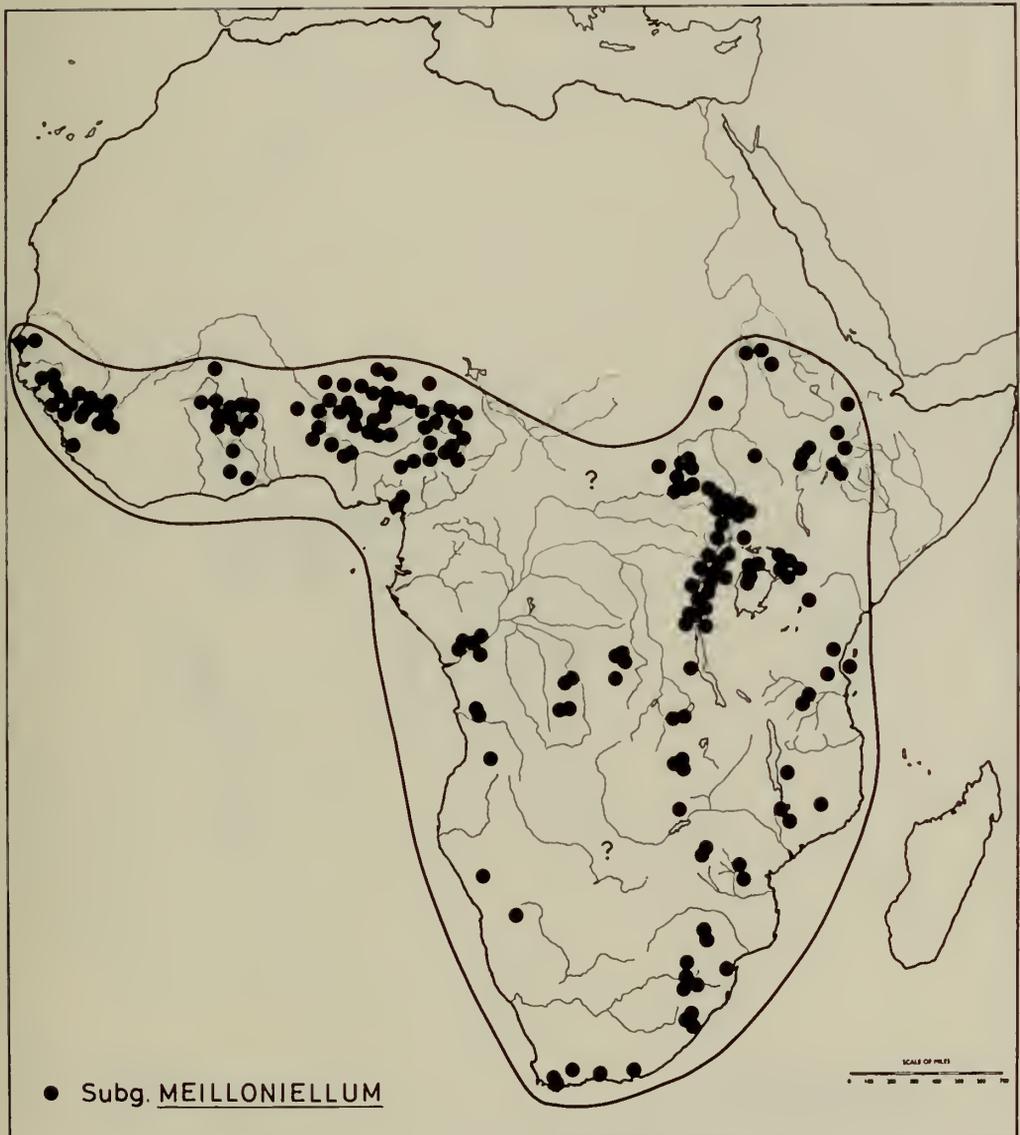
MAP 1. Distribution of the genus *Prosimulium* in Africa and its environs.



MAP 2. Distribution of the subgenus *Eusimulium* in Africa and its environs. Distribution in the African area also includes the Seychelles and Mascarene islands, just off the eastern limit of the map.



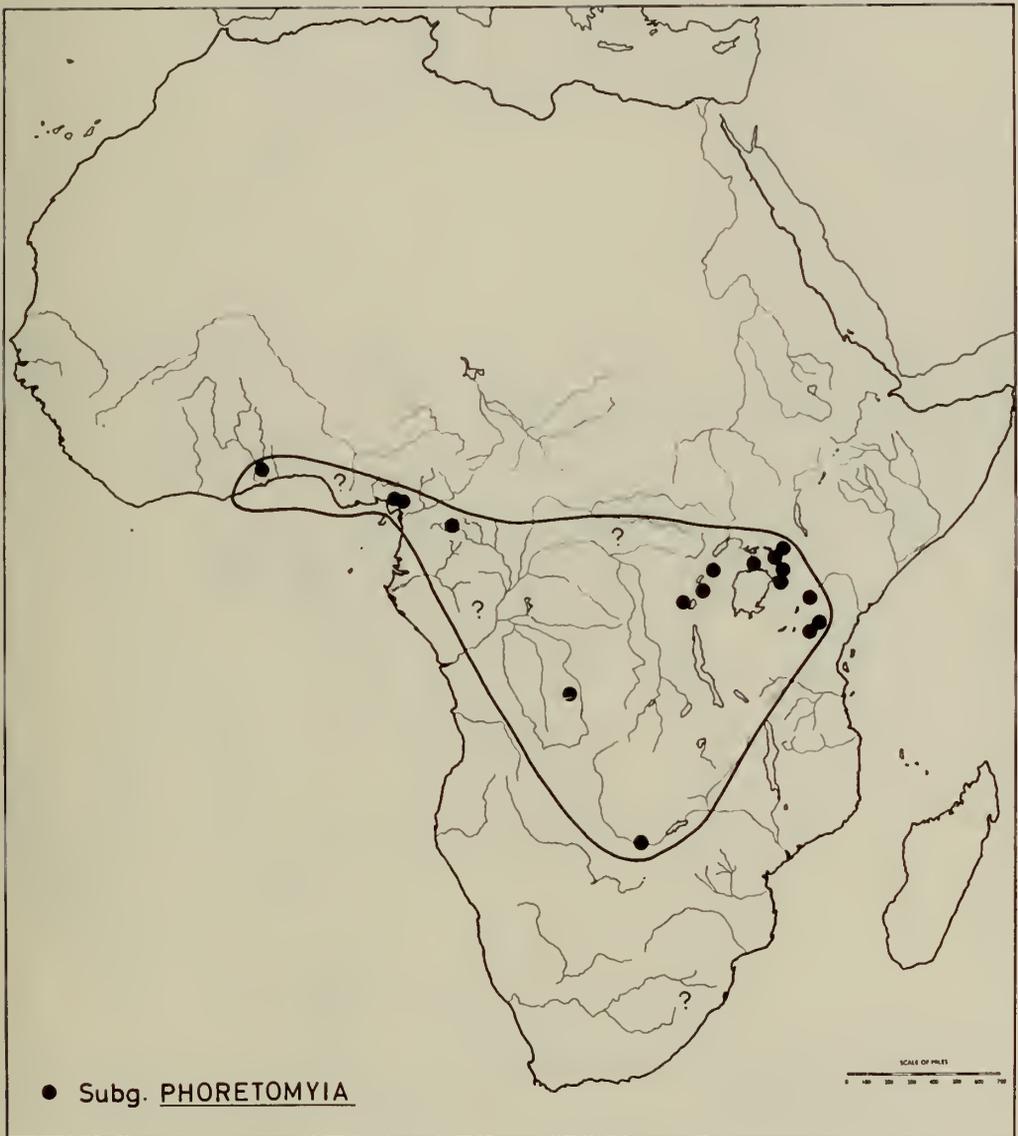
MAP 3. Distribution of the subgenus *Pomeroyellum*.



MAP 4. Distribution of the subgenus *Meilloniellum*.



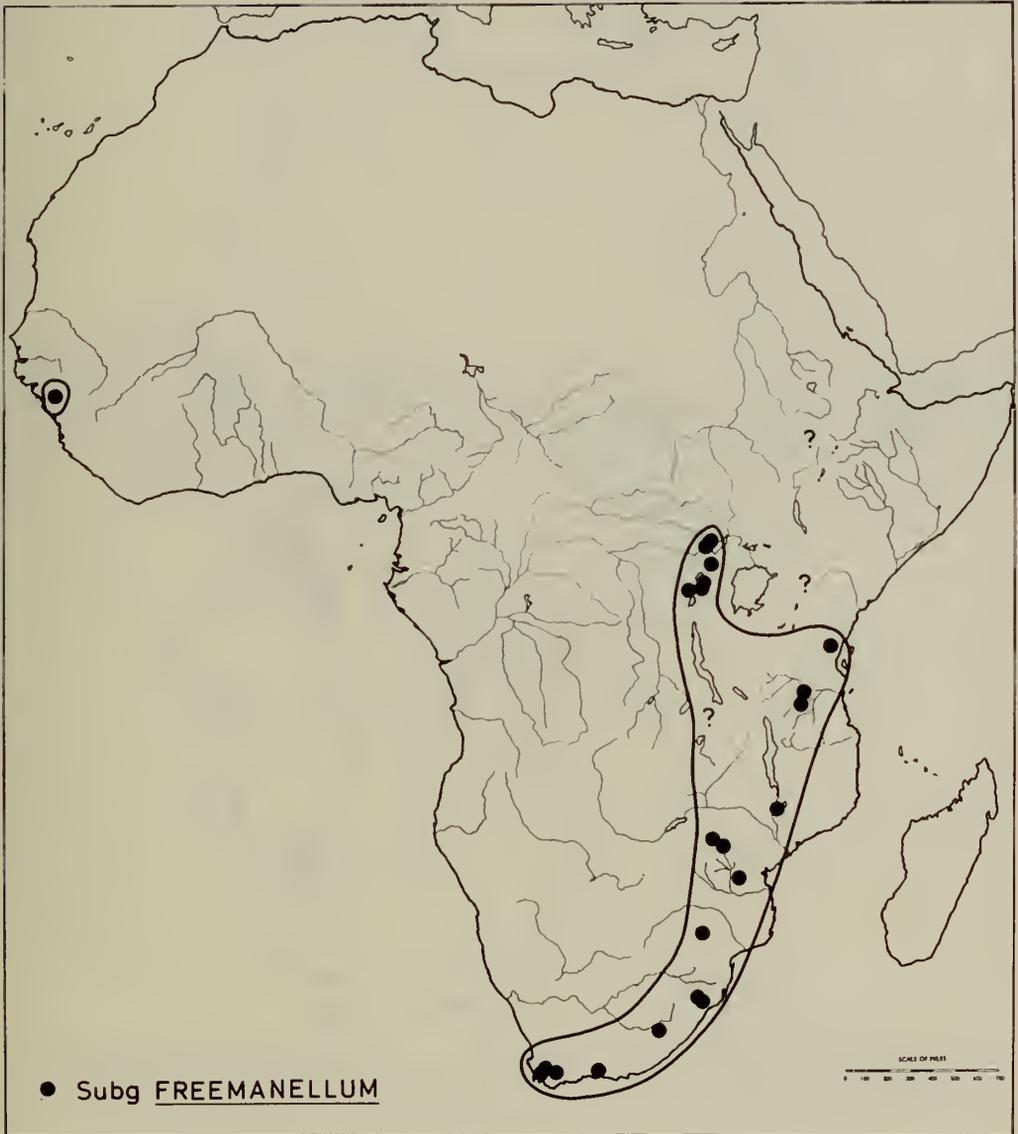
MAP 5. Distribution of the subgenus *Lewisellum*, that includes all forms living in phoretic association with crabs.



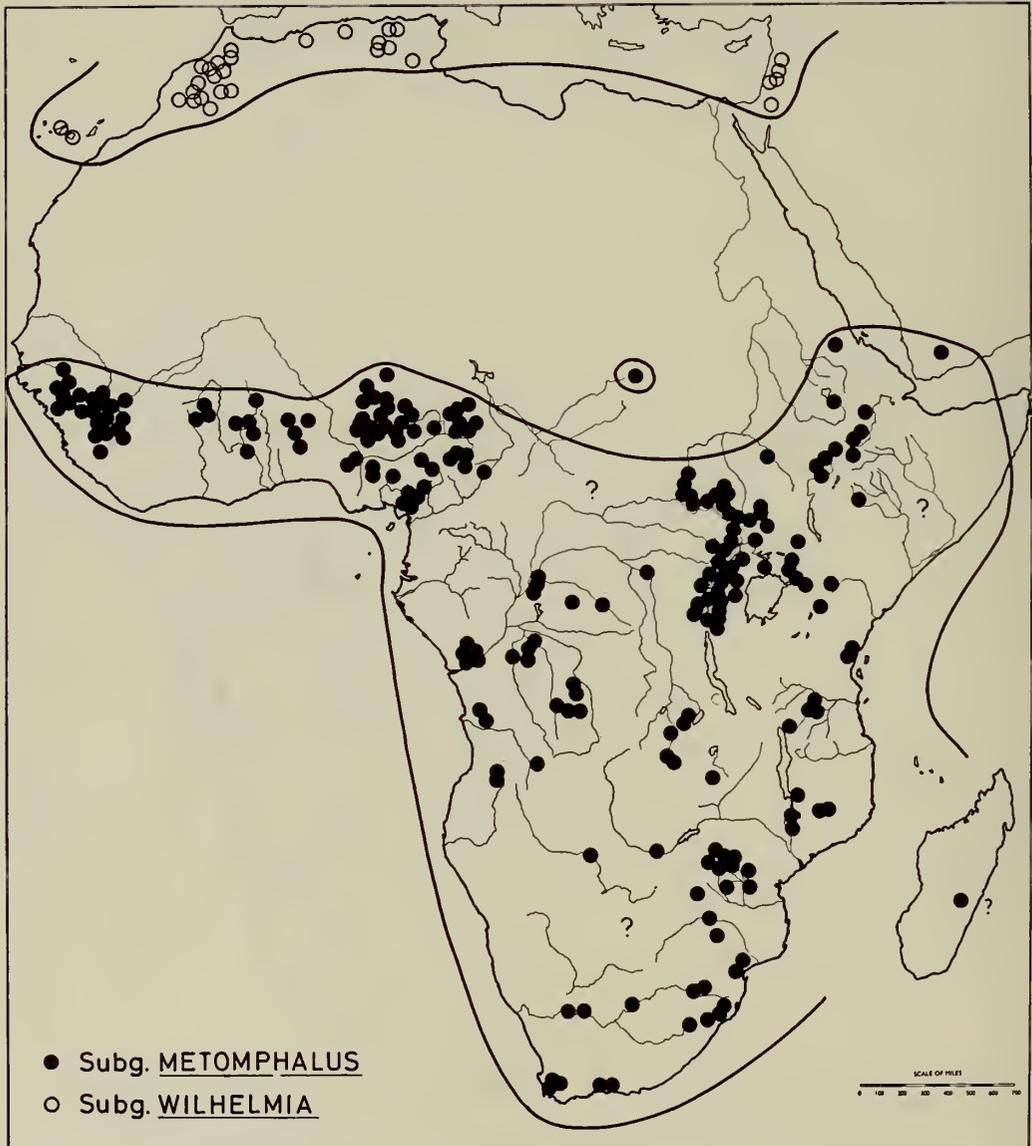
MAP 6. Distribution of the subgenus *Phoretomyia*, that includes all forms in Africa living in association with mayflies.



MAP. 7. Distribution of the subgenera *Anasolen* and *Xenosimulium*.



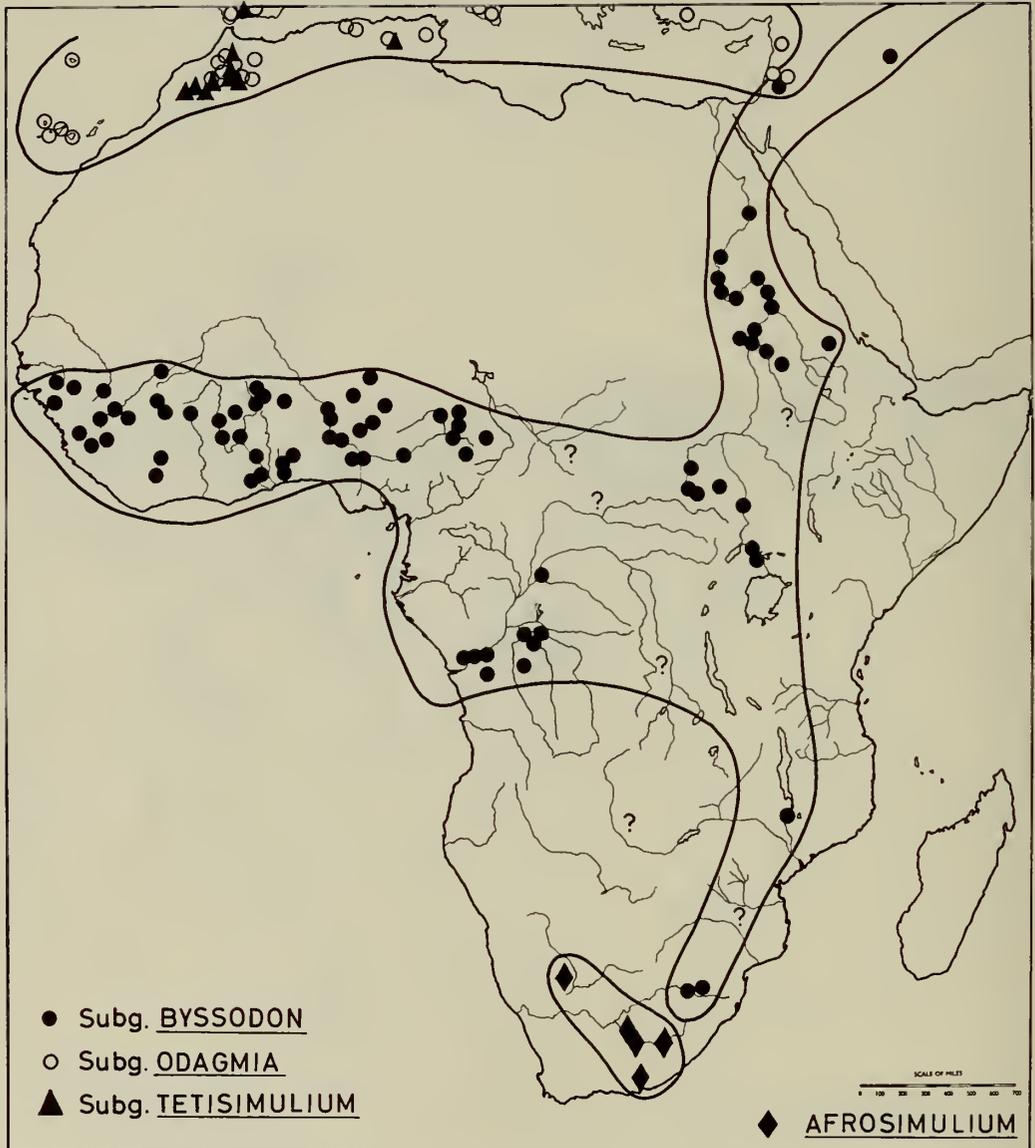
MAP 8. Distribution of the subgenus *Freemanellum*.  
Also in Northern Nigeria and Liberia (see Appendix).



MAP 9. Distribution of the subgenus *Metomphalus*, and the Mediterranean distribution of the subgenus *Wilhelmia*.



MAP 10. Distribution of the subgenus *Edwardsellum*. The species *Simulium (Edwardsellum) damnosum* occurs in all the localities for which black circles are shown, and the map therefore also shows the present known distribution of this important vector of onchocerciasis.



MAP II. Distribution of the subgenus *Byssodon* and of the genus *Afrosimulium*, and the distribution in the Mediterranean area of the subgenera *Odagnia* and *Tetisimulium*. The map shows the distribution of all Simuliidae in Africa in which the basal section of the radius is bare.

## APPENDIX

The additional information given below became available while this paper was in press.

1. Subgenus *Dexomyia* (pp. 49-55). Adult material collected by the Belgian Zoological Missions to St. Helena permits the description of *Simulium (Dexomyia) atlanticum* sp. n. to be augmented as follows:

♂ : antennae reddish-yellow on first two segments and base of third, remainder brownish. Scutellum with much long pale hair as well as some dark hair. Legs with fore coxae and all femora reddish-yellow (except for slight apical darkening), tibiae brownish but paler medially, tarsi blackish brown except for yellowish basal halves of hind basitarsi. ♀ : antennae coloured as in ♂ except that flagellum more brownish orange. Frons pale grey pruinose, occiput largely brownish pruinose. Scutum pale ashy grey pruinose over dark brown ground colour. Pleural membrane sometimes totally bare (probably naturally, and not due to rubbing). Legs coloured as in ♂ except that reddish-yellow parts more strikingly contrasting with dark parts.

The specimens seen have been labelled as paratypes and are additional type-material to that recorded on p. 55. Their data are:—

Paratypes. ST. HELENA ISLAND : 1♂, Basse Fisher's Valley, 1000 ft., 19.xii.1965, at light (MRAC, Tervuren) ; 1♀, below Diana's Peak, 22.v.1967 (MRAC, Tervuren) ; 1♂, Teutonic Hall, 1600 ft., xii.1965, at u.v. lamp (MRAC, Tervuren) ; 1♀, Teutonic Hall, 1500-1800 ft., ii.1967 (BMNH) ; 1♂, High Central Ridge, 2600-2700 ft., 11.xii.1965 (BMNH) ; 1♀, High Central Ridge, Cabbage Tree Road, 2500 ft., iii.1967 (MRAC, Tervuren).

2. Subgenus *Phoretomyia* (pp. 79-82). A new species obtained by Disney (*in press*) in Cameroun Republic lives in phoretic association with the river prawn *Atya africana* Bouvier (Crustacea : Decapoda : Atyidae) and does not fit any of the three defined species-groups on either its morphological characters or its ecological relationships. It is being described elsewhere (Lewis, Disney & Crosskey, *in press*) and assigned to a separate species-group.

3. Subgenus *Lewisellum*. Females of an unidentified species from Cameroun Republic (possibly *ovazzae*) have the yellow scaling of the abdomen largely confined to the base, and resemble females of *Phoretomyia*. They are an exception to the female abdominal characters cited for *Lewisellum* in the key (p. 39) and diagnosis (p. 76).

4. Subgenus *Freemanellum* (pp. 92-94). Adult material of the type-species, *S. (F.) berghei*, has been obtained from the Mambilla Plateau area of Northern Nigeria (collected by J. C. Deeming and H. Roberts in November-December, 1968, and sent to BMNH), and Garms (personal communication) has found *S. (F.) debegene* in Liberia. Map 8 (p. 185) and the distribution information (on p. 92) should be augmented accordingly ; the Nigerian record makes the known distribution of the subgenus *Freemanellum* much less disjunct than it previously appeared (see p. 94). The female specimens of *berghei* from the Mambilla Plateau have the pleural membrane bare, and as with *debegene*, the female sex of *berghei* may therefore have the membrane either haired or bare (it is haired in females seen from Ituri, eastern Congo) ; the males of *Freemanellum*, on present evidence, always have the pleural membrane haired.

5. The following name, published in December 1968, should be added to the catalogue of species-group names (p. 124) :

*ethiopiense* Fain & Oomen, 1968, *Revue zool. Bot. afr.* 78 : 246 (*Simulium*, as subspecies of *woodi* de Meillon, 1930). Holotype ♀, ETHIOPIA : MRAC, Tervuren.

#### INDEX TO GENUS-GROUP NAMES

The following index contains all generic and subgeneric names cited in the text, and the main entry for each genus-group segregate occurring in the African area is shown in **bold type**.

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The following index contains all specific, infraspecific, and species-group names cited in the text. Only one spelling is shown for adjectival specific names whose endings are liable to change according to generic gender (e.g. '-ensis' and '-ense' or '-tarsis' and 'tarse'), but the text may contain different endings where the original published spellings are quoted. The main entry for each recognised species-group in Africa is shown in **bold** type.

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PLATE 1

Microtrichia of the wing membrane in : A, a species of *Simulium* (*S. damnosum*), and B, *Afro-simulium gariepense*. Photographs from stereoscan microscope, magnification c.  $\times 40,000$ .



A



B